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AGE, SEX, AND WEIGHT COMPARISONS IN THREE SPECIES OF SHREWS

BY ROBERT L. RUDD

The extreme variability in species of shrews has confused systematists for some time. Shrews were conceded to be more variable than most other mammalian groups and taxonomically extremely difficult to handle. Only relatively recently have the sources of this variability been recognized and analyzed. Several recent authors have studied growth and sexual patterns in *Sorex* and related genera. These studies establish that the so-called "inherent variability" of shrews is actually no greater than that of many mammalian groups once growth and secondary sexual variation are understood. When ample specimens for comparison are available, these sources of variation cause little difficulty. The small size and the difficulty of obtaining specimens in many areas remain as the chief deterrents to full understanding of the systematics of *Sorex*.

The material presented in this paper was collected in connection with a study of differentiation in restricted populations of tidal marsh shrews in the San Francisco Bay Region. In order to compare morphological traits of several shrew populations statistically, variability due to age, sex and size (as reflected by weight) had necessarily to be considered first. Variation arising from these factors had to be eliminated or minimized before reliable trait samples could be defined and compared. This paper reports the variability of these characteristics for the individual species populations and presents data in a manner to facilitate comparisons between species. The differentiation pattern in the shrew populations under study will be presented in a later paper.

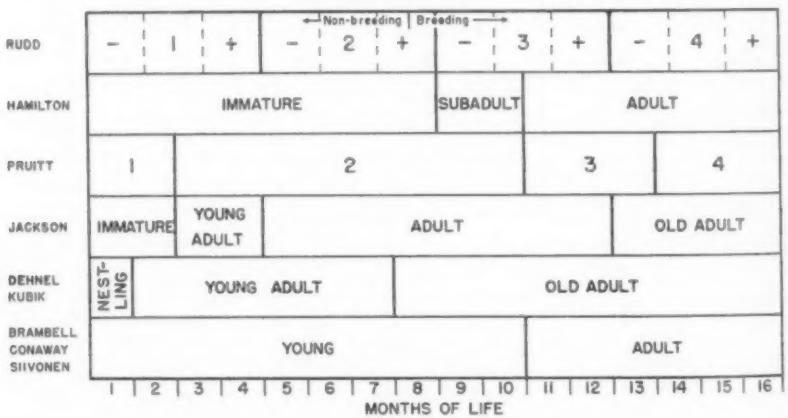
Only specimens from the San Francisco Bay Region are included. The "Bay Region" is composed of nine counties—Santa Clara, San Mateo, San Francisco, Marin, Sonoma, Napa, Solano, Contra Costa, and Alameda. All specimens from these counties for which full data were available (692) have been utilized. A number of other specimens for which full data were lacking have been used as checks but are not included in the figures presented here. Cranial terminology follows Jackson (1928). Taxonomic units included in this paper are *Sorex ornatus californicus*, *S. sinuosus*, *S. vagrans vagrans*, *S. v. paludivagus*, and *S. v. halicoetes*. Refinement of some comparisons to infraspecific levels was not considered necessary. *Sorex ornatus* and *S. sinuosus* were considered to belong to one species

group—*S. vagrans* to another. *S. sinuosus* and *S. vagrans halicoetes* were taken in tidal marshes; *S. ornatus*, *S. v. vagrans* and *S. v. paludivagus* came from either tidal marsh or upland environments.

INDIVIDUAL AGING

Method of determining age.—Relative size and relationships of cranial parts vary greatly during the course of a shrew's life time. Equivalent age groups must be compared if intrinsic genetic differences between populations are to be uncovered. For this reason an ability to estimate an individual's age from specimen material becomes important. Most authors, who have reported on age in *Sorex* have been concerned with reproductive history of a particular species and not with interspecific comparisons. Figure 1 presents a comparison of age equivalents in *Sorex* according to several authors. The purpose and method of the age determination vary in each report so that it has not been possible to compare them precisely. The age equivalents represent my interpretation of the authors' descriptions.

Attainment of sexual maturity has been used by Brambell (1935), Dehnel (1949), Hamilton (1940), and Siivonen (1954), as the critical separation point in age determination. Hamilton in addition employs hairiness, scars on the tail and tooth wear for his age criteria. As pointed out by Hamilton, shrews begin to increase sharply in size well before breeding activities begin so that size alone does not indicate breeding activity. Conaway (1952) employed tooth wear alone in determining the age of *Sorex palustris*. By totaling the height measurements of several teeth he arrived at a value which resulted in an accurate indication of age. He criticizes Pearson's method (1945) as "subjective", a criticism which must then be applied to the method reported here. Actually, I believe that close



COMPARISON OF AGE TERMINOLOGY OF SEVERAL AUTHORS

FIG. 1.—Age terminology of several authors. The terminology is that used by the author; the duration of age class is in most instances my estimation from the authors' descriptions.

familiarity with tooth structure allows a more rapid age estimation, with equal accuracy, than that obtainable by measurement. Conaway makes the important conclusion that tooth wear is relatively constant throughout an animal's life. Tooth wear, then, remains as the best single criterion of age determination in preserved specimens. Pearson (1945) described seven categories of tooth wear in the short-tailed shrew, *Blarina brevicauda*, covering a life-span of thirty-three months. His accuracy in aging *Blarina* was enhanced by observations in captivity and by recovery of marked animals. Pearson's method of determining age cannot be directly applied to *Sorex*, but my method parallels it closely. Marking and releasing *Sorex* for subsequent recapture was not considered feasible. Some information on behavior and longevity was gained from the maintenance of captive animals (Rudd, 1953).

The following method of estimating age is based entirely on cranial changes. External features such as frequency of gray hairs in pelage, hairiness of tail, number of scars on tail and length of pelage are variably expressed and cannot be employed alone with sufficient precision. In this diagnosis four major age groups, each amounting to an estimated four month period are recognized. These groups are identified by number. Individuals whose tooth wear fell into a particular numerical category but were estimated to be either younger or older than the type example were designated with a minus or a plus. Hence, three divisions of about six weeks each are recognized for each major age group. I recognize this classification simply to be one of convenience. Establishing arbitrary boundaries along a time and wear gradient can be misleading. Nonetheless, I believe the method to be sufficiently dependable to establish a reliability of plus or minus one month.

Changes apparent in the detailed diagnosis are summarized here for convenience:

Tooth wear.—Wear ranges from totally unworn in very young to worn practically to gum line in very old.

Tooth breakage.—Breakage, malocclusion, and loss of teeth are more frequent in old (3) and very old (4) adults.

Ossification.—Roofing bones in young are transparent, become translucent, then opaque. Mastoids become more massive. Sagittal suture, at first unfused, joins and, in many individuals, forms a relatively high sagittal crest. Lambdoidal suture exhibits the pattern of the sagittal suture but precedes it in ossification.

Premaxilla.—In the very young the premaxilla lies parallel to the long axis of the skull. With age it decurves sharply. An index to this curvature is the acute angle which a line across the alveolus of the anterior incisor makes with the longitudinal axis of the skull. This angle ranges from almost 90° in very young to about 30° in the oldest individuals. Strangely, the rate of decurving seems accelerated in old (3+) and very old (4) animals. The angle or slope of the anterior face of the premaxilla ranges from 40° to 65°.

Flattening of skull.—The flattened appearance of older shrew skulls is due primarily to deflation (reduction of arc) of roofing bones. Development of crests and lateral growth of the mastoids accentuate this effect. Measurements will not

describe flattening because crest development compensates for deflation of cranium.

Sex.—No sex differences other than size have been observed in skull conformation.

Diagnosis of age categories.—1− (0–6 weeks). No wear on teeth; sutures not closed along full length of midline; not closed dorsal three-quarters of lambdoidal suture; bone almost transparent; anterior incisors projecting almost directly forward; alveolar margin of anterior upper incisor almost vertical.

1 (6–12 weeks; Fig. 2A). Essentially as for 1−, but tip of metacone of Pm^3 blunted; posterior face of unicuspids scored (slightly worn—this varies considerably) but not worn to tip; sutures usually joined although weakly so (parietal

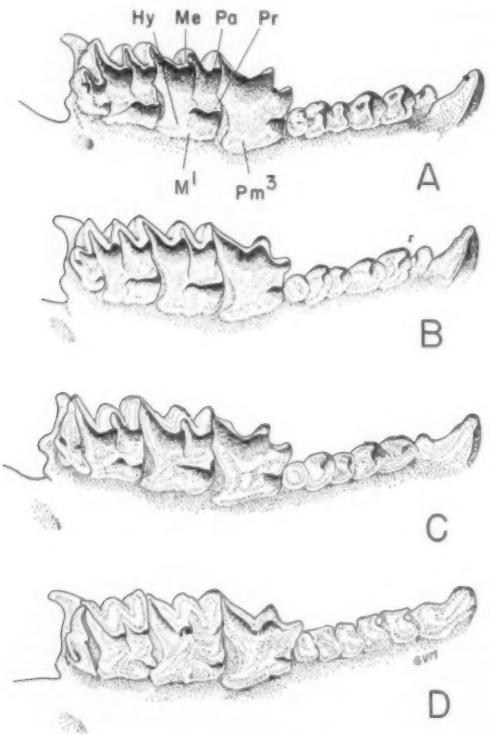


FIG. 2.—Type examples of major tooth wear categories. Age class types are all *Sorex vagrans halicoetes* in the collections of the Museum of Vertebrate Zoology. The type of class 1 (Fig. A.) is ♀ 114175; class 2 (Fig. B.), ♂ 115516; class 3 (Fig. C.), ♂ 87900; class 4 (Fig. D.), ♂ 115039. Figures represent the right upper rami viewed ventro-lingually. The designations on figure A follow Jackson (1928). Hy = hypocone; Me = metacone; Pa = paracone; Pr = protocone; M^1 = first upper molar; Pm^3 = third upper premolar. The drawing was prepared by G. Victor Morejohn.

joins first; usually lambdoidal is thinly connected); bone denser, more opaque; alveolar margin about 80° to longitudinal axis of skull; slope of anterior face of premaxilla about 40°.

1+ (12–18 weeks.) Wear on posterior faces of unicuspids reaching tips.

2− (18–24 weeks.) Wear beginning to show on molars; styles on M^3 "smoothing;" tips dulled on most cusps; cutting edge of Pm^3 (metastyle to parastyle) worn to level of non-pigmented portion of tooth; protocone and hypocone polished; bone dense, milky, opaque; sutures solidly joined; basal one-third lambdoidal suture beginning to form ridge; incisors more sharply decurved, angle alveolar margin to horizontal about 75°.

2 (24–30 weeks; Fig. 2B). Terminal pigment of metacone of Pm^3 "divided; band of wear visible along length; unicuspids usually worn across full posterior face and arcing over tips; protocones of all molars worn (as evidenced most easily by area of pigment); basal half lambdoidal suture ridged; parietals uniformly opaque, often thin in supraoccipital region; angle of alveolar margin perhaps 70°; slope of anterior face of premaxilla 45–50°.

2+ (30–36 weeks). Essentially as type 2; band of wear appearing on cutting face of M^1 and M^2; metastyle of M^2 seems to "flow" into (has worn to same level of) paracone of M^3; lambdoidal ridge developed for basal one-half to two-thirds, may be strongly joined if not partially ridged for remainder.

3− (36–42 weeks). Unicuspids worn over entire face; tips may be worn entirely from posterior unicuspids; usually some wear on lingual face also; M^1 and M^2 show broad band of wear on ventral face (the area between styles and cones is "hollowed" out); pigment on mesostyles of M^1 and M^2 gone or nearly so; lambdoidal crest well-formed basal two-thirds; angle of alveolar margin 60°–65°.

3 (42–48 weeks; Fig. 2C). Unicuspids show wear on both anterior and posterior faces (arcing over tips); non-pigmented portions of molars strongly hollowed out (effectively sharpening pigmented styles?); protocones of M^2 and M^3 worn smooth or nearly so; pigment usually reduced in area or absent; whole effect of occlusal faces is of smooth rounded surfaces; lambdoidal crest heavy basal three-quarters; sagittal crest beginning development; angle of alveolar margin of incisor about 55°–65°; slope of anterior face of premaxilla 50°–55°.

3+ (48–54 weeks). Essentially as type 3 with greater wear on occlusal faces; cusps on M^3 worn almost flat; usually slight amount of pigment on mesostyle of M^3; hypocone of Pm^3 hollowed out like shallow buttonhook; lambdoidal crest may reach to midline (weaker dorsal one-quarter); sagittal crest formed along entire line of juncture; angle of incisor alveolar margin 50°–60°; slope of anterior face of premaxilla 55°–60°.

4− (54–60 weeks). Some unicuspids may have worn so that occlusal surface of one contacts worn surface of next tooth; pigment gone on M^3, barely present in other molariform teeth; occlusal surface on M^3 not only flattened but somewhat hollowed; crests well formed; basal one-half lambdoidal crests particularly heavy.

4 (60–66 weeks; Fig. 2D). All unicuspids flat on occlusal surface; often unicuspids missing (3 missing in Fig. 2D); all molars present flattened occlusal

surface with low hillocks representing original cusps; small amount of pigment may remain in positions of protocone, metacone and paracone of M^1 and M^2; M^3 may be hollowed shell; mesostyle of M^3 still connecting with parastyle of M^2; lambdoidal crest heavy to midline; sagittal crest well-developed but weaker than lambdoidal; bone in thin areas opaque; incisors directed almost straight down; angle of incisor alveolar margin to horizontal axis about 30°–40°; angle of slope of anterior face of premaxilla 60°–65°.

4+ (66–72 weeks). An exaggeration of type 4; no hillocks remaining on occlusal faces of molars; slight amount of pigment may remain along metastyles; mesostyle of M^3 may be so worn that M^3 is completely separated from M^2; incisors shell-like because of wear on posterior occlusal surfaces; crests and density of bone at maximum; teeth often broken or missing; angle of incisor alveolar margin seemingly about the same as type 4.

Duration of life.—There is little evidence that the normal lifespan of *Sorex* exceeds sixteen months. Hamilton (1940) indicates that some animals may reach seventeen months. A specimen described by Montagu (1922) had extremely well-worn teeth and a grizzled coat lending evidence to his contention of a long life span. I have seen two individuals, both of which were captive for several months and which showed the same characteristics as Montagu's specimen that were probably seventeen to eighteen months old. Attainment of such an age is not the rule. Indeed, most animals die before reaching twelve months of age. It has seemed reasonable for practical purposes to consider sixteen months as the maximum life span. With this assumption, I have compared the age terminology of several authors (Fig. 1). Other insectivores live for greater lengths of time but *Sorex*, regardless of its geographic origin, seems to exhibit the same aging pattern. *Sorex araneus*, *S. fumeus*, *S. cinereus* and *S. palustris* parallel closely the aging pattern that is found in the three species of shrews described herein.

SEX AND AGE COMPOSITIONS OF THE SPECIES POPULATIONS

Sex composition.—Individual age estimations have been plotted by species on a calendar scale in order to facilitate comparison of reproductive and population information. Figure 3 illustrates the composition of the *vagrans* group which here includes 443 individuals of *Sorex vagrans vagrans*, *S. v. paludivagus*, and *S. v. halicoetes*. Charted in Figure 4 are 248 individuals of *S. ornatus californicus* and *S. sinuosus*. The calendar scale begins with the month of March during which the first young appear, and continues through the following February.

Some precautionary comments regarding age estimation and sexing are necessary at this point. Shrews are notoriously difficult to sex externally. Only breeding adults can be easily sexed by superficial examination. Individuals in age categories 1 and 2 are best sexed by dissection. By seven months of age males may be easily sexed externally, but sexing of females is sure only by internal dissection. This practice has not been observed by many collectors of shrews. Fortunately, well over 500 of the specimens reported on here were collected within recent years by workers especially careful to record sex correctly.

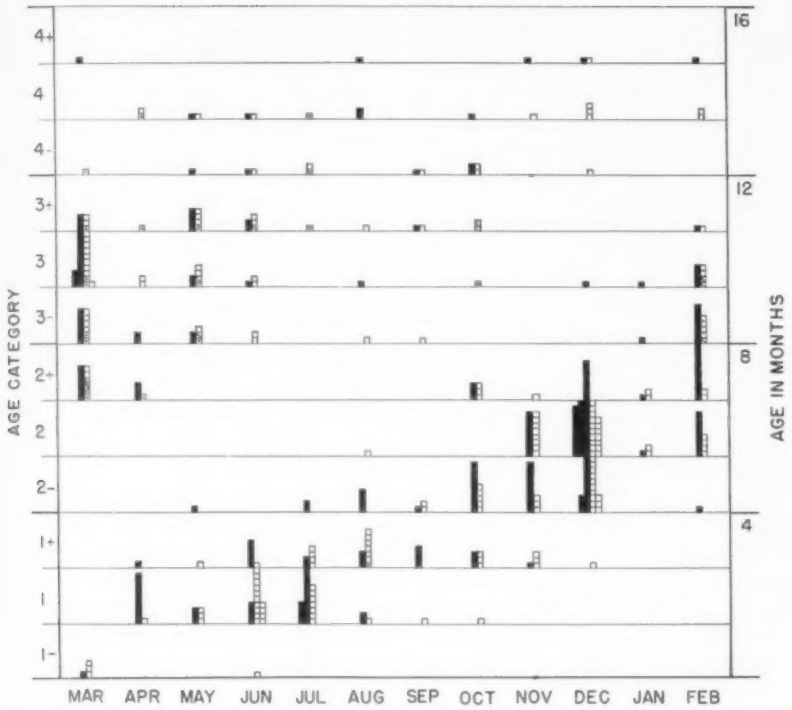


FIG. 3.—Sex and age composition of the *vagrans* group. Solid squares represent males; hollow squares, females. Pregnancy is indicated by a dot within the square; lactation is indicated by a diagonal line.

Two sources of error appear in the estimations of ages figured here. Absolute ages may not be accurate. I allow an error of plus or minus one month and believe that this margin of error is sufficiently liberal. One major error is present and should be considered when drawing conclusions from the figures. Age categories 1− and 4+ in each chart have about the same specimen representation. At first glance, one would suppose that actual occurrence in the population was reflected by specimens plotted. This decision is probably correct for category 4+ but it is certainly not correct for category 1−. This method of aging relates age to the time of birth and not to the appearance of young in traplines. Shrews are normally weaned at 16 to 20 days, although captive animals have been weaned at 14 days. Weaned animals appear to remain in or near the nest with other litter members for another week or two. Accordingly, there is only a slight chance that shrews under a month in age would appear in traps. Those individuals figured in age category 1− are probably five to six weeks old. All other age categories are presumably properly represented.

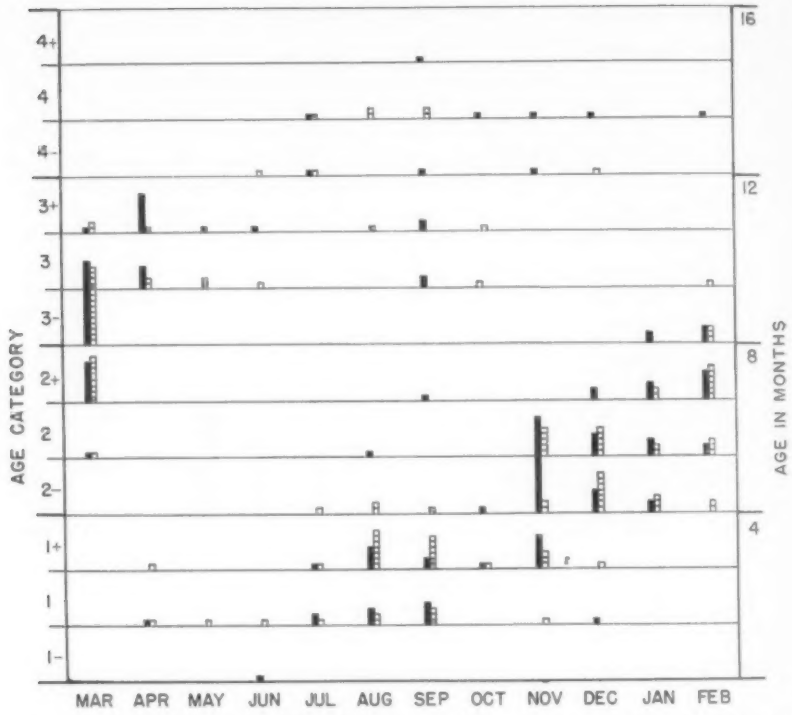


FIG. 4.—Sex and age composition of the *ornatus-sinuosus* group. See Figure 3 for description.

Males occur in traplines in slightly higher frequency than females. In this sample of the *vagrans* series 242 (54.6% of total) are males and 201 are females (120.4 males:100 females). The percentage closely approximates that found in *S. araneus* by Brambell (1935) who had well over a thousand trapped animals in his sample. I found that males were not markedly more frequent in spring-taken samples. Brambell found the percentage for April and May males to be 67 and 62 respectively. He attributes the disparity in sex ratio during these months to differential selection of sexes by the traps and notes that this period is characterized by the first estrus in the female. The first estrus apparently appears in March in this area and for this month the sex ratio in *S. vagrans*, the larger sample, approximates 1:1. In the *ornatus-sinuosus* series the ratio is almost precisely 1:1. The total *ornatus-sinuosus* series exhibits a percentage of males of 51.6. There are 128 males and 120 females in this sample. Middleton (1931) described an overall male percentage of about 61 in *S. araneus* (156.4 males:100 females). The ratio of males was higher among old animals. Greater general activity of sexually mature males was suggested to explain this ratio. In the

specimens which I have studied, the overall sex ratio is lower and the sex ratio in old animals is the reverse of that which Middleton describes. Figure 5 (upper) shows graphically the relation of sex to age. Only material from the *vagrans* series is included. Data are grouped into three-month periods in order to enhance reliability. Monthly frequencies in both species groups vary considerably. How much of this variation derives from sampling technique is impossible to say. In general, however, there seems only to be a slight overall preponderance of males which when studied more closely proves to be confined to immature animals. The critical month is March. Numbers during this month are about equal and previous patterns are reversed following March. This description seems to apply to both species groups.

Breeding season.—Almost all pregnant females appear in March through April although pregnancies have been recorded from the last week in February to the last week in October. A few adult females may rear second litters but I have little evidence to indicate this. It is probable that females born late in the prior year do not breed until late the following spring or summer. The appearance of young in late summer or early fall is probably accounted for by these fall-born adults and by a few young of the year, presumably born two to five months previously, which appear on the charts as pregnant in August and September. Curiously, there are several more pregnant females of age category 1 and 2 in the *ornatus-sinuosus* series than in the *vagrans* series. This may amount to a species difference. Perhaps correlated with this is the apparent later breeding period of the *ornatus* group. The data for spring-taken pregnant animals in the *ornatus* group are, unfortunately, meager. Employing incidence of age-group 1 shrews as a criterion, one can see that these are most common in late summer in the *ornatus* series while they appear more frequently in late spring and early summer months in the *vagrans* series. Biological reasons for such a difference can only be guessed at. An ecological difference may be the basis of it, for many of the *ornatus* charted are from upland environments subject to greater seasonal changes than the relatively stable fresh- and salt-water marshes characteristically preferred by *vagrans*.

Although small differences exist, both species series seem to have essentially the same aging pattern. To be sure, the somewhat later breeding period of *ornatus* is reflected noticeably on a calendar scale. However, the rate at which aging takes place and the composition of age classes seems to be essentially the same.

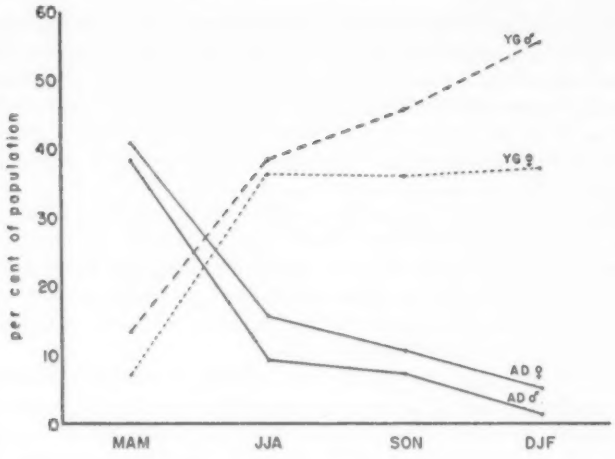
Age class frequency.—With the exception of the slightly delayed breeding season in the *ornatus* series there are apparently no significant differences in age and sex composition of the two species groups. With the material available it was considered justifiable to combine sexes and lesser age categories in order to arrive at age class frequencies in the population at large. Combined data from Figures 3 and 4 are presented in Figure 5 (lower) as frequency graphs. Frequencies are based on 691 specimens, with full data, collected within the geographic scope of this problem. Major age categories are indicated on the left and frequencies on the right. The calendar scale begins with March, as in Figures 3 and 4, but is extended over a twenty-five month period. Monthly frequencies in the last

thirteen months on the scale are duplications of those appearing in the first twelve months. This method of presentation allows observed age composition of the population to be expressed well beyond the probable maximum life span of individual shrews.

Frequencies of age groups in the population are based on trapped individuals. As indicated above, shrews younger than five or six weeks of age seldom appear in traplines. It would be reasonable to bring the age group 1 value to at least 20 per cent of the total. Such a figure would apply to March when the first young appear and be added to in April and May as the March-born young mature and as new young appear. If one accepts certain assumptions, it is possible to make rough calculations to arrive at a correction factor appropriate at least for March. Assume the sex ratio in the adults in March as 1:1 (this is approximately the observed ratio). The same ratio must also be assumed for newly-born young. In the *vagrans* series about one-third of the adult females are pregnant or lactating in March. With a gestation period of about 21 days most pregnant animals may be expected to give birth during that month. We have scarcely any information on early success in nest-building and parturition but we do know that litters of *S. vagrans* found in the field usually consist of four to six young. By assuming the production of four young from each pregnant or lactating female, we can calculate that 40 per cent of the entire population must be young animals. The pregnancy incidence is higher in April and this month's production would be added to the March 40 per cent figure. Since age group 1 covers four months, the production of May and June must be added in like manner. Juvenile mortality has not been considered in these figures and it probably is high. Halving the calculated percentage value yields a more reasonable figure of 20 per cent for March. Values for April, May and June would be correspondingly higher. Figure 5 (lower) is based only on specimen populations and does not include corrections for probable population composition in the wild.

Some months are represented by relatively few specimens and account for irregularities in the frequency distribution. January frequencies, for example, are based on only 17 specimens with full data, neither age groups 1 nor 4 being represented in this sample. A larger sample should indicate a slight frequency of each of these age classes. September frequencies, based on 36 specimens, show a seemingly high number of "adult" and "old adult" shrews in the population. These September frequencies may be affected by a slight incidence of late summer breeding in young of the year. Other monthly frequencies appear to be accurate. For example, the lack of age-group 1 in the February sample is probably accurate, since this sample comprises 65 individuals. In another instance, only one individual of age-group 3 was observed in the December sample comprising 115 individuals. This frequency is undoubtedly close to the actual occurrence (of this age group) in the population.

Frequencies graphed here provide convincing evidence of population turnover which is essentially complete within twelve months following the breeding season. Slightly over 80 per cent of July-taken shrews are young of the year while most of the remainder are animals estimated to be fourteen to sixteen



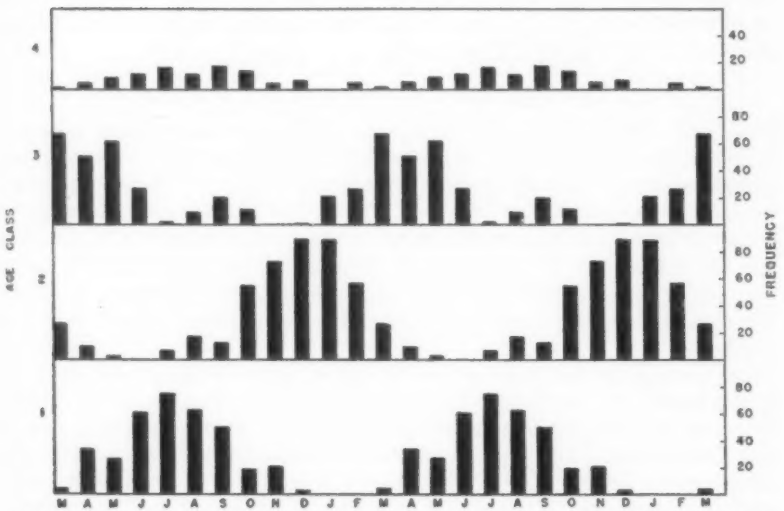


FIG. 5.—UPPER: Frequency of age and sex groups in *Sorex vagrans* by trimonthly periods. In this figure "AD" represents adults, that is, animals from the previous year; "YG" indicates young of the year. Less data are available from the *ornatus* group but the pattern, described here for *vagrans*, is about the same. LOWER: Composition of the entire shrew population by age classes. Combined data derive from Figures 3 and 4. Further description in text.

months old. This latter group would represent animals born in late spring of the prior year. Only rarely does an individual born during the spring of one year survive until the fall of the next. September seems to be the critical month for these animals. July records the highest frequency of age-group 4 individuals, but during no month of the year is the incidence of "old adults" above 18 per cent. Frequencies of this class throughout the year vary the least and seldom amount to 10 per cent of the sample.

The composition of a given monthly sample may be roughly predicted if age estimations are reasonably accurate. Hence, animals born in March, April and May probably account for the bulk of breeding animals the following spring. Animals born in late summer, at which time there is a slight increase in breeding activity, probably account in the following year for the increase in group 3 representation in August through October.

If numbers of shrews in the sample were equally distributed throughout all the months of the year and if the actual frequency of age-group 1 in the population were known, it would be possible to calculate survival prospects for each age class. Such calculations seem futile with the limitations enforced by the present data. Nonetheless, the data presented here, supported by several authors, show that shrews are annual animals almost totally replaced each year at the close of the breeding season. To my knowledge there is no evidence of wild-taken *Sorex* surviving through a second winter.

WEIGHT COMPARISONS

Weights of shrews have little value in separating population types. Indeed, it is difficult to distinguish the species concerned in this problem by weight alone. For this reason, weight data are not treated statistically. Monthly weight averages, ranges and numbers are presented in Table 1. Data are grouped under currently recognized species. Patterns of weight change are shown for the three species in Figure 6. For purposes of these charts, animals appearing before January 1 were considered young; those appearing after January 1, adults. Weights were recorded only if collection data and sex identification were complete.

Earlier collectors often did not record weights. Most of the weights presented in this paper are derived from specimens taken by S. B. Benson, O. P. Pearson, or myself and are considered accurate. Nonetheless, these weight data, as with most weight information on field-collected small mammals, must be taken with certain reservations. Variations due to sex and age are to be expected and show up well on the figures. Males of all species tend to be heavier than females during the early part of the breeding season but may not be heavier at other times. Individuals increase in weight with advancing age but this increase cannot be seen easily in those older than two or three months, until the breeding season begins. Variation because of starvation or dehydration probably exists, but I have no evidence of its extent. Shrews collected by kill-trap methods and weighed shortly after collection probably represent actual weights. Those collected in live-traps not supplied with food and water usually die and presumably lose

some weight due to starvation and dehydration. Variation from these last-named causes may be sufficiently extreme to mask real differences in weight due to age, sex or species.

Comparisons would be simple if equal numbers of all forms were available for

TABLE 1.—*Monthly weight data for three species of shrews*

		VAGRANS			ORNATUS			SINUOSUS		
		Wt. range	Mean	Nos.	Range	Mean	Nos.	Range	Mean	Nos.
Jan.	Ad♂	3.4–4.4	4.05	2	3.4–4.7	4.17	3			
	Ad♀	3.4–4.0	3.81	4						
Feb.	Ad♂	4.2–8.4	5.95	10	4.5–6.3	5.42	4	3.6–4.6	4.1	2
	Ad♀	2.8–6.4	4.39	15	3.3–5.6	4.25	4	3.2–3.6	3.37	3
Mar.	Ad♂	3.4–7.5	5.9	15	4.9–7.7	5.86	10	5.4–6.9	6.31	8
	Ad♀	3.2–7.7	5.01	19	4.1–5.6	4.80	15	4.0–4.6	4.36	5
Apr.	Ad♂	3.2–4.2	3.8	5	4.6–5.8	5.21	8	5.7–6.8	6.25	2
	Ad♀				4.0–5.7	4.45	4			
	Im♂	3.6–4.6	4.2	3		3.1	1			
	Im♀	4.4–4.5	4.45	2	3.5–3.8	3.65	2			
May	Ad♂	4.8–6.8	6.3	6						
	Ad♀	4.6–7.0	6.18	4		5.2	1		6.7	1
	Im♂		3.6	2						
	Im♀					3.8	1			
June	Ad♂	4.4–4.8	4.6	3						
	Ad♀	5.7–7.0	6.43	3						
	Im♂	3.7–5.0	4.22	3						
	Im♀	4.1–5.1	5.19	7		3.5	1			
July	Ad♂		5.6	1				5.0–6.0	5.5	2
	Ad♀	5.6–6.7	6.15	2					5.6	1
	Im♂	4.0–4.3	4.19	9					3.8	1
	Im♀	4.0–4.7	4.55	4				3.8–4.5	4.07	3
Aug.	Ad♂	4.3–7.2	5.53	3						
	Ad♀								6.2	1
	Im♂	3.6–6.5	4.83	6	3.3–3.5	3.4	2	3.6–4.1	3.9	5
	Im♀	3.0–5.7	4.21	7	2.9–5.1	3.34	7	4.1–6.2	4.6	5
Sept.	Ad♀		6.9	1		5.3	1	5.2–5.8	5.47	3
	Im♂		5.4	1	3.5–4.5	3.86	3			
	Im♀				3.0–4.8	3.96	3		4.3	1
Oct.	Im♂	4.0–6.2	4.9	7		4.0	1		4.1	1
	Im♀	3.2–5.8	4.49	10		3.0	1			
Nov.	Im♂	3.4–4.2	3.74	13				3.3–5.9	4.5	12
	Im♀	3.3–4.0	3.52	14	3.4–3.9	3.6	5	3.7–5.2	4.43	3
Dec.	Ad♂		6.2	1						
	Im♂	3.4–6.4	4.94	46	4.0–5.5	4.75	2			
	Im♀	4.2–6.2	5.12	30						

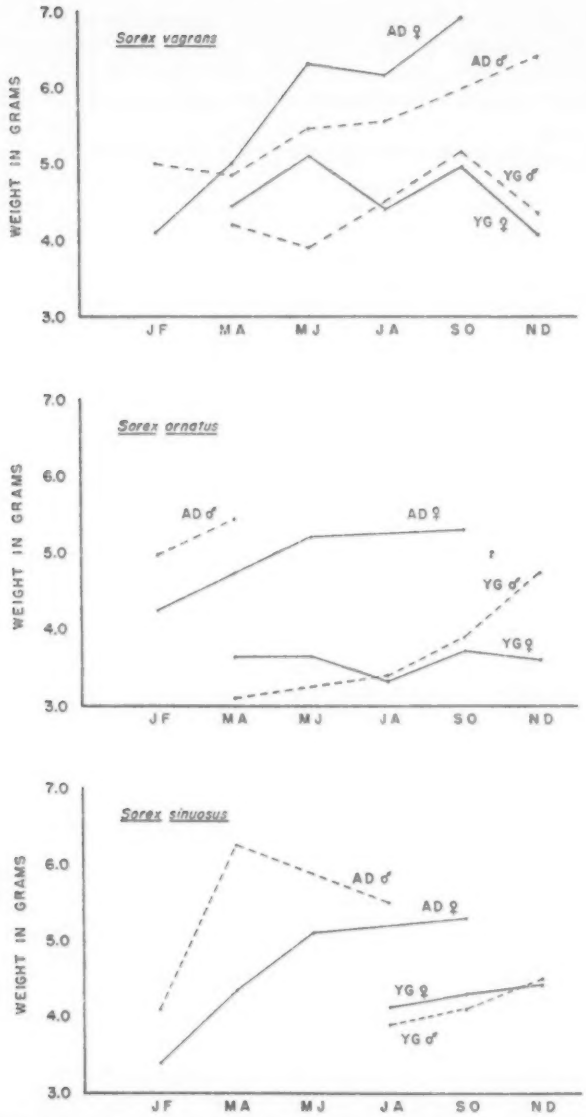


FIG. 6.—UPPER: Weight comparisons by sex and age in *S. vagrans*. Points represent bi-monthly averages. See Table 1 for additional data and text for further description. MIDDLE: Weight comparisons by sex and age in *S. ornatus*. LOWER: Weight comparisons by sex and age in *S. sinuosus*.

all months of the year. Lacking such data, strong reliance should not be placed on comparisons presented here. Nonetheless, some observations can be made on the charted data. Animals of all species taken in February, March and April are largest. Although the range within a given sex may be great, sexual differences during these months are pronounced. This pattern accords with those described for *S. araneus* (cf. Brambell, 1935; Dehnel, 1949) and *S. fumeus* (cf. Hamilton, 1940). December and January-taken males are slightly larger than females taken during these months. Sex differences, with one exception for the remaining months, are not easily discernible. The exception concerns post-reproductive animals. Numbers of these are few, but apparently males decline in weight after breeding, whereas females continue to grow well after the peak of breeding.

Species differences in weight are weakly indicated. In *S. ornatus* no female exceeds 5.8 grams although males may reach 7.7 grams. No male *ornatus* weighing less than 3.1 grams or female weighing less than 2.8 grams was observed. Maximum weight of *S. sinuosus* males was 6.8 grams, of females 6.7 grams. Minimum weights of *sinuosus* were males, 3.4 grams, and females, 3.3 grams. Maximum weights of males of *S. v. vagrans* was 8.4 grams, of females, 7.7 grams; minima were 3.2 grams for males and 2.7 for females. *Sorex v. halicoetes*, in general larger than the parent species *vagrans*, shows a lesser weight range. Maximum weight for males was 7.2 grams, for females, 7.0 grams; minima were 3.1 and 2.7 respectively.

Maximum weights of all forms were achieved by adult shrews (individuals born the prior year); minima, with one exception, were all recorded for young of the year. Extreme weights, then, do represent differences in age, but intermediate weights cannot be relied upon to separate breeding animals from young of the year.

Of questionable importance is the observation that several *S. v. vagrans* young of the year are sufficiently heavy to fall into the breeding adult weight category, whereas none of the *ornatus-sinuosus* individuals do. This condition may result from incomplete data rather than from a real difference in growth rates between species groups.

It would be tempting to place the larger animals in the "more favorable" environments. Salt marsh shrews are generally larger than their upland counterparts and upland animals from verdant regions seemingly are larger than those from arid portions of the species' range. In general, a relationship between size of individuals (and, for that matter, numerical size of populations) and stable, lush environments does exist, but there are exceptions to this rule.

SUMMARY

A technique for determining the age of individual shrews is presented. Amount of tooth wear is the basic criterion for judgment, although several other cranial characteristics have also been employed. Four major age classes are recognized each of which covers about four months of life. This aging technique permits the analysis of certain population characteristics. Population data are plotted for three species of San Francisco Bay Region shrews (*Sorex ornatus, S. sinuosus*, and *S. vagrans*).

In March, the sex ratio in all three species approximates 1:1. Adult females apparently live somewhat longer than adult males. Among adults, females dominate in late spring and summer samples. Young males begin to predominate over young females in fall samples and from December to February this domination becomes marked.

Breeding apparently begins later in the spring in the *ornatus-sinuosus* group than in the *vagrans* group. Breeding in the year of birth occurs more often in ornate shrews than in vagrant shrews but in neither does it occur commonly.

All species of *Sorex* seem to be annual animals dying shortly after the breeding season. Few animals live longer than one year. By midsummer, young of the year have almost replaced the adult breeding population.

Only during the breeding season are sexual differences in weight marked. Males are noticeably heavier during the early part of the breeding season but apparently gain little weight later in the spring. Females continue to gain weight slowly until death. Young increase in weight at a phenomenal rate for the first few weeks, but after about eight weeks, change little until the onset of the breeding season. Weight increases at this time are accomplished rapidly. Young males become heavier three to four weeks before the females, paralleling the pattern of onset of sexual activity. Ecological differences may explain in part some differences in weights of restricted populations. Marsh shrews are less subject to fluctuations in cover and food supply than upland shrews.

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OBSERVATIONS ON THE BIOLOGY OF *SOREX TROWBRIDGEI* IN THE SIERRA NEVADA, CALIFORNIA

By E. W. Jameson, Jr.

Recent years have seen the publication of life history studies for several kinds of soricid shrews, and we now have some idea concerning some of the salient biological features of these animals. There is an abundance of species of shrews, sometimes several species living in one locality, and it is a reasonable assumption that their habits are different. Also, it is not unlikely that some geographically widespread species will differ within themselves ecologically as well as morphologically, such differences reflecting responses to variations in their environments. As natural history studies of shrews gradually become more extensive and detailed, it may be possible to discover discrete biological differences among the various kinds and also to learn to what degree the environment may alter the biology of any one kind.

The data here are not extensive, but concern one species, *Sorex trowbridgei*, in the Sierra Nevada of California. In some respects, especially with regard to the reproduction, *trowbridgei* appears to vary from some species of *Sorex* studied by other investigators. It is hoped that this account may serve also to describe any biological characteristics of *trowbridgei* that may be different in other parts of its geographic range.

Habitats.—The Trowbridge shrew is common in the coniferous woodlands of the Sierra Nevada up to elevations of 5000 feet in Plumas County and at least to 6000 feet in Tuolumne County to the south. This forest is comprised of large coniferous trees (*Pinus lambertiana*, *P. ponderosa*, *Pseudotsuga menziesii*, *Abies concolor*, and *Libocedrus decurrens*); the less conspicuous woody plants are smaller deciduous trees (*Quercus kelloggii* and *Acer macrophyllum*) and shrubs (*Quercus vaccinifolia*, *Alnus rubra*, *Ceanothus* spp. *Cornus* spp., and *Ribes* spp.). The ground litter is composed of the decaying debris from these plants and provides the home and hunting ground of *trowbridgei*. In areas where the forest has been removed, either by logging or fire, the land is revegetated by brush or small coniferous trees; in these areas shrews persist in lesser abundance. *S. trowbridgei* is not typical of wet meadows in the Sierra Nevada; this environment is inhabited by *S. vagrans*; the water shrew (*S. palustris*) is confined to the borders of streams and small bodies of water, and in these situations *trowbridgei* and *palustris* occur side by side. From the accounts in the literature, one can assume that the habitat

of *trowbridgei* does not vary greatly throughout its range. Elsewhere in California (e.g., along the coast), this shrew is associated with a very different flora; but this environment is a mature forest type with an abundant ground litter for foraging shrews, and thus resembles the habitat of *trowbridgei* in the mountains.

Food.—Stomachs of eighty *trowbridgei*, collected at all seasons, indicated that it resembles some other species of *Sorex* in subsisting mostly on small arthropods. Seventy-three stomachs contained food, most of which was sclerotized insect material, finely masticated.

One can imagine that these tiny predators grasp at any small arthropod on the forest floor, for there is a great variety of insects, spiders, and centipedes in their diet; Neuroptera, Coleoptera, Diptera, Lepidoptera, Heteroptera, and Hymenoptera were recognized. Spiders and centipedes were found only in shrews taken during December. Annelid worms also were taken in the autumn and winter months but such food is doubtless difficult to obtain in the dry summer months. Planarians were found in stomachs of two shrews. Moore (1942) emphasized that *trowbridgei* may consume seeds of Douglas fir (*Pseudotsuga menziesii* (= *taxifolia*)). Fourteen stomachs of this shrew trapped by Moore in coastal Oregon contained more than 60 per cent plant food. Unidentified seeds were found in stomachs of four winter-trapped shrews from Plumas County.

Molt.—The two pelages of the Trowbridge shrew are markedly different; although there is some variation, the summer pelage is a dark shade of brown and the winter coat is gray. These are described in detail by Jackson (1928) who noted that the spring molt may begin as early as April, but more commonly occurs in late May or June; his earliest molting specimens were taken along the coastal regions of British Columbia, Washington, and Oregon, whereas those showing late molt were taken in the Sierra Nevada of California. In the northern Sierra Nevada (Plumas County) the spring molt (of the adults, from gray to brown) may take place at any time in June, July, or August. Only five molting adults were taken, one in June, three in August, and one in September; two of these specimens actually represented the fall molt, for they were acquiring the gray pelage; a few very old shrews live long enough to grow a second winter coat. The fall molt may occur between August and November, but most of the molting specimens were taken in October; a few molting shrews were trapped in September and one each in August and November. In this molt the young of the year acquire the gray coat which replaces the brown pelage. The heavier winter coat probably serves to protect the wearer from cold temperatures, so it is not surprising that shrews keep this pelage from September until June in the higher mountains.

Age classes.—In order to discuss population structure, one must establish certain age classes. For this account a shrew is considered to be either young or adult, although it is possible to separate several different groups according to a variety of morphological criteria. Generally, the students of shrews have somewhat different interests and use different criteria and age groups. Valid criteria for distinguishing relative ages of shrews may differ from one species to the next, even within the genus *Sorex*; and some characters seen readily in freshly trapped

specimens cannot be discerned in museum skins. Failure to appreciate that such variables exist has caused some workers to be overly critical of the criteria used by their colleagues.

For this discussion immature shrews are those trapped in the year of their birth and adults are shrews born the previous year; in other words, January first is arbitrarily set as the date at which a shrew becomes adult. Such a date is not especially significant in the annual cycle of shrews; but it is a time of little growth and no perceptible reproductive activity, and the population then consists of only one age class.

There is little difficulty in separating the two generations of *trowbridgei*; at most times of the year one age group predominates, and the two groups are quite distinct in the spring when both may be commonly trapped. In general, the characters of adult *trowbridgei* are the same as those applied by Hamilton for *fumeus* (1940); some of these criteria cannot be used as easily, if at all, for *palustris*, *vagrans*, and perhaps other species of *Sorex*. In shrews there is continuous tooth wear and no tooth growth; therefore there is a great difference in the degree of wear seen in young and adults during the spring and summer months. Age groups can be distinguished by this feature alone. The difference in pelage between the two age groups is also a useful criterion. Virtually all adults are gray because very few individuals live long enough to molt during their second summer. The young shrews are brown until their first molt in September, at which time any surviving adults would be very aged and show extreme tooth wear. Hamilton (*op. cit.*) observed that in the late winter and springtime adult

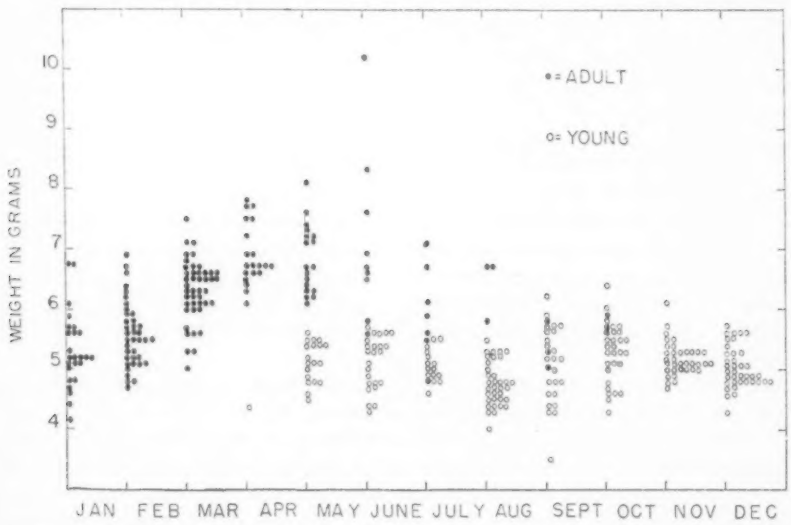

FIG. 1.—Monthly changes in weights of *Sorex trowbridgei* in the Sierra Nevada of California.

TABLE 1.—*Seasonal occurrence of adult and young Sorex trowbridgei (by percentages) collected in the Sierra Nevada, California*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Spet.	Oct.	Nov.	Dec.	Total
Adults	24	32	39	27	18	9	8	3	4	3	0	0	165
Young	0	0	0	1	19	25	15	35	27	28	35	38	223
Per cent adults	100	100	100	96	49	38	35	8	13	10	0	0	

fumeus gradually lose the pencil of hairs at the tip of the tail; the same obtains for *trowbridgei* with the exception that very old shrews may have a new pencil of hairs after their second molt. In addition, weight is usually sufficiently greater in the adults so that it alone serves as a very useful means of separating the young shrews from the adults (Fig. 1). The weight of breeding adults far exceeds that of the young; but after July the few adults found are likely to be in a non-breeding condition, and they will be little, if any, heavier than the young. At this time, differences in tooth wear are pronounced, and the old shrews exhibit adult characteristics in their pelage and reproductive tracts, rendering age classification rather simple.

The Trowbridge shrew is a short-lived creature and the annual population turnover is completed by late summer. Probably eighteen months is close to the maximum life span in the Sierra Nevada; the mean life span must be much less. They live sufficiently long to bring forth a new generation, and after May the proportion of adults to immatures drops rapidly (Table 1). In this study a few adults were caught in the summer, but less than two per cent of the 165 adults was taken after August. These aged shrews must surely find feeding difficult for their teeth are worn virtually to the cingulum. Expressed in a percentage of adults in the population (Table 1), this figure is a measure of both the decrease of adults and increase of young. Some workers have suggested that the disappearance of adults is an illusion caused by the "dilution" of the population with young animals, but it is quite apparent that in *trowbridgei* there is a very real and sudden decrease of adults in late spring and early summer (Fig. 1).

This short life span is typical for several kinds of soricid shrews that have been studied by various workers. Differences in this pattern which may be characteristic for the several species of shrews will probably be found in the rapidity with which adults disappear. Unfortunately, published data are not expressed as in Table 1 and a closer comparison between *trowbridgei* and other species cannot be made.

Reproduction.—*Sorex trowbridgei* recalls other species of long-tailed shrews in the general pattern of its reproductive behavior, but there are several features in which it appears to be distinct. The information in this account is based upon gross examination of carcasses; there are no data on the histological changes of the reproductive structures, hence this summary, especially with regard to the females, is far from complete. This series of 388 shrews is a small sample but sufficient to show that *trowbridgei* is, reproductively, generally similar to some other species of *Sorex*, but from this series one cannot delimit in detail the specific

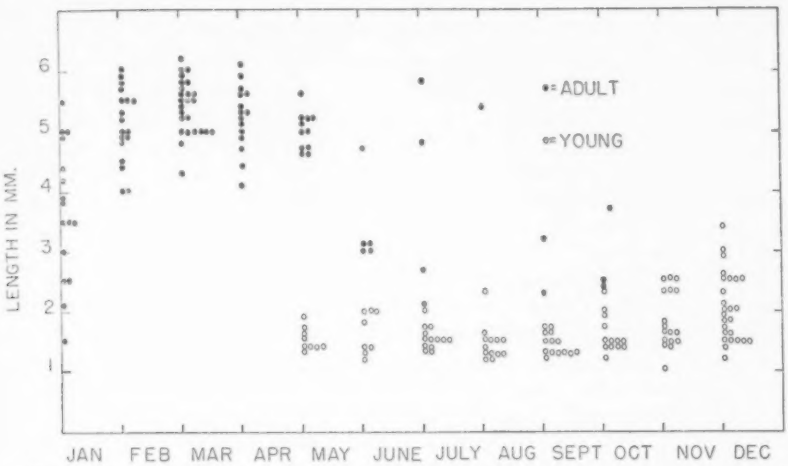

FIG. 2.—Monthly changes in length of testes of *Sorex trowbridgei* in the Sierra Nevada of California.

differences. Nevertheless, an attempt has been made to discuss the breeding season, the frequency of embryos, and some other aspects of the reproduction of these shrews.

Both sexes mature rapidly in February when there is a coincident increase in weight and sudden development of the reproductive structures (Figs. 1–3). This occurs when the snow is deep and freezing temperatures prevail. The data for the three year period are pooled by months. Some variations are clearly apparent to the field worker, but the sample is too meagre to be convincing. For example, it appeared that reproduction began at least one month earlier in 1951 than in 1949; also, that shrews living in the south-facing brushfields commenced breeding at least one month ahead of those living in the dark coniferous forest 200 yards away. Breeding activity decreases in the latter half of May, and most adults

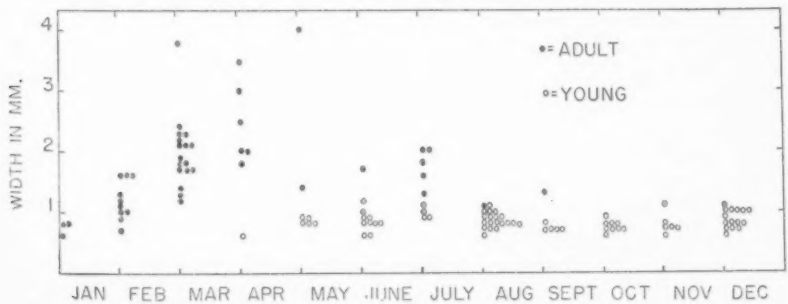

FIG. 3.—Monthly changes in width of uterine horn (measured at the basal third) of *Sorex trowbridgei* in the Sierra Nevada, California.

taken later are in a post-breeding condition. One adult male in August was apparently fecund. The earliest date on which embryos were observed was February 25, 1951, but all other pregnancies were found in April or May. Reproduction ends in June for most individuals, but one late breeder was taken on August 8, 1951; this individual was lactating and weighed 6.5 grams, and it was captured in the same trapline as the previously mentioned male of that date.

There are several discrete changes in the reproductive structures at the beginning of the breeding season. There is a pronounced increase in the weight of both sexes: non-breeding adults weigh between 4.0 and 5.5 grams, males then being slightly heavier at this time. In breeding condition most shrews weigh between 6.0 and 7.5 grams, and gravid females may be considerably heavier. The testes of immature males, collected in the autumn, are from 1.0 to 3.0 mm. in length, but in breeding males they measure from 4.7 to 6.0 mm. or more (Fig. 2). The prostate glands develop more rapidly than the testes and exhibit a greater disparity in size between the breeding and non-breeding condition. During June the reproductive structures shrink and become non-functional; such males weigh little more than young of the year, but are easily recognized by their olive-colored, flaccid testes and greatly worn teeth.

Female *trowbridgei* appear to attain sexual maturity about two weeks after the males. This relatively slight difference is difficult to discern because female shrews exhibit few signs of fecundity that are apparent to the field naturalist. Non-breeding females are characterized by rather slender, whitish uterine horns that are from 0.6 to 1.2 mm. wide each. By the first half of March this structure had grown to a width of from 1.7 to 1.9 mm., and in the latter half of that month it ranged from 2.1 to 3.8 mm. wide (Fig. 3). It appears that an individual is fecund if the uterine horns are 2.0 mm. or more in width, because in such instances the accompanying ovaries contain fresh corpora lutea. Probably these enlarged uteri actually represent early stages of pregnancy, for Brambell (1935) found a continued uterine growth following estrus and prior to implantation in *Sorex araneus*.

The breeding season of *trowbridgei* appears to begin earlier and to terminate sooner than that of some other kinds of *Sorex*. Hamilton (*op. cit.*) showed that *S. fumeus* breeds from April through the spring and summer until August; and cited two instances of breeding in October. Brambell (1935) observed that breeding extends from May to October in *S. araneus* of the Old World. Similarly Moore (1949), in a summary of breeding records for *S. cinereus*, indicated a breeding season beginning in April and ending in October. Apparently the water shrew, *S. palustris* resembles *trowbridgei* in the early onset of breeding; Conaway (1952) found, by histological examination, that some males had testes with sperm as early as late January, and that breeding may continue until July (females) and August (males), but his sample was small. According to Dalquest (1938) a rather long breeding season, extending from late January until November, obtains for *S. vagrans* in Washington. Only eight gravid females of *trowbridgei* were taken; it appears that these animals are rather secretive during pregnancy. The mean number of embryos per female was five; extremes were three and six. One female examined had recently given birth to one young.

Post-partum pregnancies are probably rather frequent in this shrew, but they are difficult to recognize by gross examination. Of the eight visibly pregnant females, four were also lactating; and numerous other lactating shrews had uterine horns from 2.0 to 3.0 mm. in width, suggesting that they contained very young embryos. This phenomenon has been observed in other soricid shrews by several workers (Brambell, 1935; Conaway, 1952; Hamilton, 1940); and it occurs in a variety of small rodents and insectivores (Hamilton, 1949). There can be little doubt that some kinds of small mammals commonly produce two or more litters without interruption. In *trowbridgei* two or three litters produced successively might compensate for the rather short breeding season and general lack of reproductive activity during the summer.

SUMMARY

Sorex trowbridgei is a common forest-dwelling shrew; it occurs sparingly in brushlands and cutovers. Arthropods comprise the bulk of the food; earthworms and planarians are sometimes eaten. The fall molt occurs from August to November, but most often in October; a few adults acquire a second summer (brown) pelage in June, July, or August.

The Trowbridge shrew is short-lived; adults disappear rapidly during May, June and July. Breeding extends from February until early June, after which time most of the remaining adults are in a non-breeding condition. The mean number of young was five; extremes were one and six. Evidence indicates that post-partum pregnancies are rather frequent.

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REPRODUCTION IN THE WOLVERINE, *GULO GULO*

By Philip L. Wright and Robert Rausch

The reproductive habits of the wolverine, largest of the terrestrial mustelids, have remained largely unknown. In the American literature there are scattered statements indicating that the young are born in the spring and that the number of young at birth is from two to four (Seton, 1927). Seton also states that mating takes place in March and the young are born in June. These statements, which are only partially correct, have come largely from woodsmen who have made no detailed study of the species. Mohr (1938, 1939) states that breeding occurred between July 17 and 22, 1915, in a pair of captive European wolverines kept at the Copenhagen Zoo and the female gave birth to a litter on February 17, 1916. The same female produced another litter on February 24, 1917 after breeding the previous summer. She suggests that the European wolverine has a gestation period of about nine months. Recently Rausch (1953) has concluded that the American and European wolverines belong to the same species (*Gulo gulo*). The above evidence and the known occurrence of delayed implantation with the accompanying long periods of gestation in several mustelids suggest that this species should be more thoroughly investigated.

The collection of Alaskan mammals carried on under the direction of the junior author since January, 1949, is an important activity of the Animal-borne Disease Branch of the Arctic Health Research Center. The material thus far obtained has been utilized for studies of diseases and helminth parasites, and has provided information of interest to mammalogists. In the course of these collections Rausch obtained several wolverines in 1949 and 1950 and some female reproductive tracts were sent to Wright for study.

In species in which breeding occurs in mid-summer and the young are born the following spring, the reproductive tracts of those females destined to produce young in the spring will show no macroscopic signs of pregnancy if the animals are killed in the fall and early winter. If the ovaries and uteri are histologically sectioned, inactive corpora lutea will be found in the ovaries and unimplanted blastocysts in the uteri (Hamlett, 1935, Wright, 1942). When histological examination of one of the first tracts obtained from a female wolverine showed corpora lutea and unimplanted blastocysts, it was decided to study reproduction as fully as possible in this species.

We are indebted to Drs. H. W. Mossman and C. H. Conaway who examined the slides, read the manuscript, and made numerous helpful suggestions.

MATERIALS AND METHODS

The wolverines examined by Rausch to date, more than 50 in number, have been secured largely through the cooperation of trappers. Never an abundant animal, the wolverine is continuously persecuted, and since July 1, 1953, the Territory of Alaska has paid a bounty on this animal. The animals were examined soon after death, or were frozen until examination was possible. After recording

TABLE 1.—*Findings in female reproductive tracts of Gulo*

Date killed	Weight of ovaries		Distribution of corpora lutea		Remarks
	Right	Left	Right	Left	
Oct. 18, '53	243	244	1	3	2 blastocysts, 1 dead embryo
Nov. 1, '51	143	152	2	2	4 blastocysts
Jan. '50	28	63	—	—	
Jan. '50	158	180	2	2	4 blastocysts
Jan. 20, '53	291	303	2	3	3 embryos, 1 resorbing embryo R, 3 L (22 mm. CR)
Jan. 25, '50	160	157	—	—	
Jan. 26, '53	107	110	—	—	
Feb. 2, '53	430	420	2	2	4 embryos, 2 R, 2 L, 2 ♂♂, 2 ♀♀ (68 mm. CR)
Mar. 21, '52	89	95	—	—	
Apr. 9, '53	202	199	4	0	Lactating; placental scars—2 R, 2 L
Apr. 10, '53	179	220	4	0	Lactating; placental scars—2 R, 1 L

appropriate measurements and other data, the animals were autopsied in order to collect internal parasites and other materials. The genital organs were fixed in 10 per cent formalin or A.F.A. The skulls and bacula were cleaned by dermestid beetles and bleached in hydrogen peroxide. All the skeletal material was handled uniformly. This report summarizes data from 22 males and 11 females obtained in northern Alaska from the fall of 1950 through the fall of 1953. The fixed reproductive tracts and the cleaned skulls and bacula were sent to Wright who studied the material.

Female tracts.—The ovaries were dissected free from the surrounding bursa, weighed to the nearest milligram, dehydrated in dioxan, infiltrated and imbedded in paraffin, and serially sectioned at 10 microns (Table 1). Representative sections were stained in hematoxylin and eosin or Groat's quadruple stain, and the slides studied. If corpora lutea were found in the ovaries of animals without macroscopically visible embryos, the upper third of the corresponding uterine horn was cut off, serially sectioned, and the sections searched for blastocysts. If blastocysts corresponding in number to the corpora lutea in the ovary were located, no further sectioning of that uterine horn was done. If all the blastocysts were not located in the first piece of uterus, the middle third was handled in the same way, and even the basal third was sectioned in some cases. Measurements were made of the corpora lutea and the blastocysts with an ocular micrometer and by counting the number of sections through which the structures extended.

Male tracts.—Each testis was dissected free of the tunica vaginalis, the vas deferens cut off close to the testis, and the combined weight of the paired testes and epididymides taken. A portion of one testis and the tail of the epididymis was cut out, sectioned, and stained. The presence or absence of sperm in both the testis and epididymis was determined.

Skulls and bacula.—Many of the usual cranial measurements were taken and

the skulls were studied for characters that might be useful in estimating age. After cleaning, the bacula were allowed to dry for several weeks and weighed to the nearest milligram.

OBSERVATIONS

Females.—The female reproductive tract is typical of the Mustelidae. The ovary is enclosed in a bursa but there is an ostium out through which a portion of the fimbria extends. The uterus is bicornuate and the common lumen of the body is quite short. The fixed uterine horns in immature animals taken during the winter are about 60 mm. long by 3 mm. in diameter. In adults taken in fall or early winter the horns are about 90 mm. long and 5 mm. in diameter. No os clitoridis could be located macroscopically in the one adult vulvar region preserved.

The ovaries of immature females taken during the fall and winter months are without corpora lutea or large follicles. The cortical and medullary regions are distinct. The outer cortex shows many primary follicles and some medium sized follicles. The remainder of the cortex which comprises the largest portion of the ovary consists of large masses of interstitial gland cells, many of which develop from the theca of atretic follicles forming corpora atretica. Other cords of interstitial gland cells extend from the stroma of the tunica albuginea to the medullary stroma and these cells are probably derived from the stroma. The medulla is fibrous with numerous blood vessels and scattered clumps of small interstitial gland cells.

The ovaries of adult females taken during the fall and early winter tend to be somewhat larger than those of the immatures and they show inactive corpora lutea (Pl. I). There are one to three corpora per ovary and they are from 1.65 mm to 2.00 mm in diameter on the stained slides. The corpora do not bulge from the surface of the ovary and they are not distinctly visible externally, but they could be seen easily macroscopically if the ovary were sectioned with a razor blade or sharp knife. The cells of these corpora are small, and in the November and January specimens are vacuolated like those seen in the corpora of winter killed marten (Wright, 1942). The cortical interstitial tissue is well developed in all three of the animals in inactive pregnancy and comprises the largest portion of the ovary. The medullary interstitial cells are especially well developed in the October specimen. They occur as scattered cords of large glandular cells. The October specimen shows some small follicles with antra and many corpora atretica, but the November and January specimens are without follicles with antra, and atretic follicles still showing degenerating eggs are extremely rare.

The ovaries of the two animals in active pregnancy are the largest (Pl. I). Their corpora range from 3.38 mm. to 3.60 mm. and they are nearly seven times the volume of the inactive corpora of specimens taken earlier in the season before implantation. These corpora are very conspicuous externally in the intact ovary and some even appear to be attached to it by short pedicles only. The corpora are highly vascularized and show very large secretory cells without vacuoles.

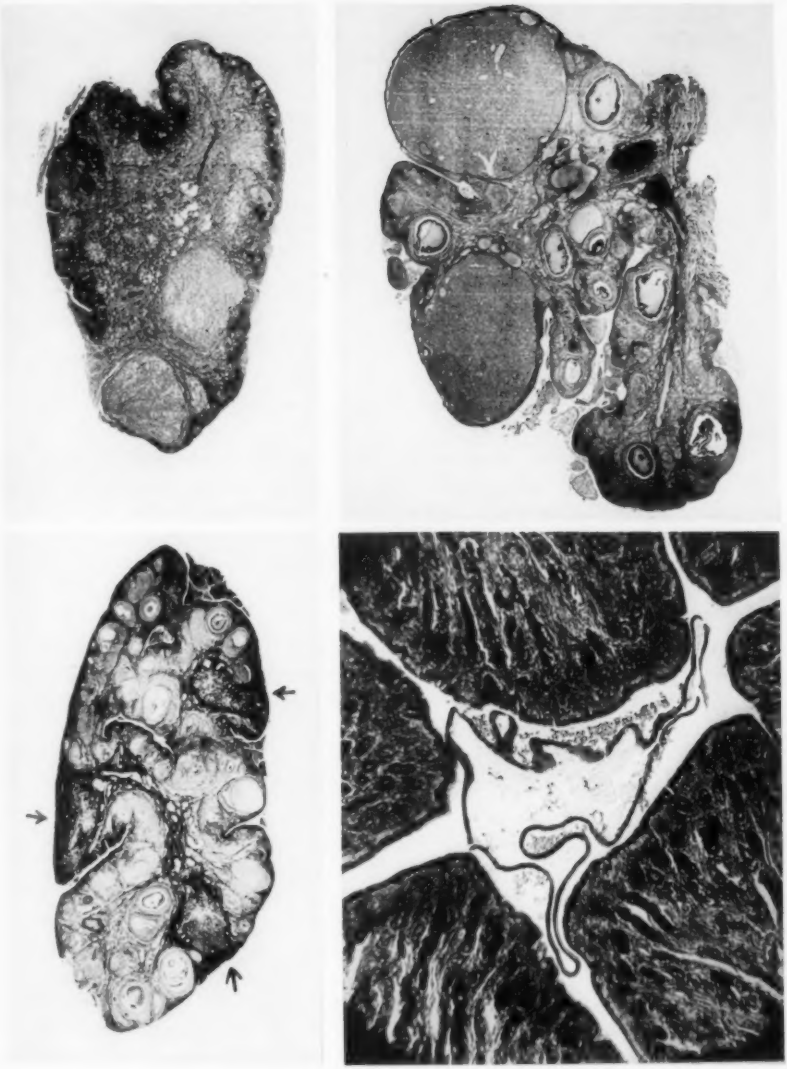

PLATE I

UPPER LEFT: Ovary of adult female with unimplanted blastocysts, showing two inactive corpora lutea. Animal killed in January. About 8.5 ×. UPPER RIGHT: Ovary of adult female with 68 mm. CR embryos showing two large active corpora lutea. Animal killed February 2. About 8.5 ×. LOWER LEFT: Ovary of adult female during lactation showing three degenerating corpora lutea (shown with arrows) and absence of large follicles. Animal killed April 9. About 8.5 ×. LOWER RIGHT: Blastocyst of wolverine in situ in the lumen of the uterus. The conspicuous zona pelucida surrounds the embryo. Several nuclei can be seen within the embryo. From animal killed October 18. About 77 ×.

TABLE 2.—*Summary of information on position, size, and numbers of cells in wolverine blastocysts*

Date killed	Position of blastocyst	Dimensions in microns	No. of cells counted
Oct. 18, '53	Up. ⅓ L. U.	783 x 513 x 840	673
	Low. ⅓ L. U.	810 x 378 x 611	387
Nov. 1, '51	Up. ⅓ R. U.	1053 x 880 x 108	1024
	Up. ⅓ R. U.	1485 x 1120 x 189	987
	Up. ⅓ L. U.	1283 x 870 x 189	1077
	Mid. ⅓ L. U.	999 x 590 x 378	873
Jan. '50	Mid. ⅓ L. U.	615 x 459 x 202	47
	Low. ⅓ L. U.	1290 x 1013 x 1188	630
	R. U.	1188 x 940 x 189	980
	R. U.	1012 x 620 x 270	1513

The interstitial tissue has undergone considerable regression. There are numerous medium-sized follicles.

The ovaries of the two lactating females show degenerating corpora; in one case they are scarcely recognizable (Pl. I). These ovaries consist mainly of interstitial cell masses or corpora atretica. The interstitial cells are more numerous than in the active pregnancy stages. The lack of large follicles and the general inactivity of these ovaries makes it clear that the female wolverine does not have an estrous period shortly after parturition as has been reported for the fisher (Hall, 1942).

Placental scars could not be seen externally in the two tracts of lactating animals but when the uteri were bleached in hydrogen peroxide and dehydrated and cleared in methyl salicylate the ring-shaped scars could be seen distinctly.

The uterus of one of the animals with unimplanted embryos appeared somewhat larger and the macroscopic blood vessels were conspicuous. Histologically the blood vessels showed thick hyalinized walls and it is thought that this animal may have been parous.

Description of the blastocysts.—Ten blastocysts were located in the three adult animals taken during the period of inactive pregnancy (Pl. I). The most conspicuous thing about these embryos is the heavy zona pellucida, about 7.8 microns in thickness, which can be seen even in the freshly mounted unstained ribbons. The embryos are lying completely free in the lumen of the uterus, and all are partly collapsed and some completely so. They are well enough preserved so that nuclear counts can be made but not well enough to distinguish between inner cell mass and trophoblast cells. They are similar to the blastocysts of field-preserved marten (Wright, 1942) but are larger and have more cells. Information on size, distribution, and cell counts is summarized in Table 2.

There is a great variation in the size of these blastocysts and in the number of cells of which they are composed. It is difficult to estimate their original size before collapse but they were probably about 2 mm. in diameter. The blastocysts may be at any position in the lumen of the uterus and the spacing of the embryos prior to implantation has not occurred in any of the animals. In the two lactating animals migration of some of the embryos from the right to the left uterine horn

TABLE 3.—*Findings in male reproductive tracts of Gulo*

Date killed	Weight of baculum	Estimated age	Paired combined weight of testes and epididymides	Presence of sperm
July 22, '52	462	Juv.	1775	None
Oct. 28, '51	1160	Im.	1743	None
Nov. 1, '51	2755	Ad.	4160	None
Nov. 1, '51	735	Im.	1365	None
Nov. 1, '51	Incomplete	Ad.	2098	None
Dec. 10, '51	1780	Ad.	1980	None
Dec. 11, '51	653	Im.	—	—
Dec. 27, '51	1015	Im.	1698	None
Jan. 6, '52	1890	Ad.	3225	None
Jan. 19, '52	2475	Ad.	3325	None
Jan. 25, '52	1359	Im.	1075	None
Feb. 4, '53	2022	Ad.	8640	Spermatogenesis beginning, no sperm in epididymis
Feb. 21, '52	1175	Im.	3400	None
Feb. 28, '52	920	Im.	1645	None
Feb. 28, '52	2483	Ad.	4480	None
Mar. 25, '52	1373	Im.	1355	None
Mar. 26, '53	1215	Im.	3300	None
Mar. 31, '53	1458	Im.	5020	Few sperm in testis, none in epididymis
Mar. 31, '53	1009	Im.	—	—
Apr. 4, '52	1429	Im.	6110	Few sperm in testis, none in epididymis
Apr. 4, '52	2940	Ad.	14070	Active spermatogenesis, some sperm in tail of epididymis
Apr. 16, '53	1242	Im.	2530	None

had occurred since all of the corpora lutea were in the right ovaries and placental scars were found in the left horns of both animals.

In two of the animals in inactive pregnancy a blastocyst was located for each corpus luteum. In the other, only two blastocysts were found although there were four corpora in the ovaries. In this case one small structure, 170 microns in greatest length, with distinct zona pellucida was found. There are small bodies within the zona which do not stain and it is thought that this is an embryo that died during cleavage. The other potential embryo was not located but it may have been lost if it were lying very close to one of the cuts made in preparing the uterus for imbedding.

The general picture of reproduction in the female wolverine can be seen from the data derived from the seven adult animals. Breeding takes place sometime between April and October, likely in midsummer. Development of the embryos is arrested when the blastocyst stage is reached and the embryos remain in this condition until January when implantation occurs. The young seem to be born in late March or early April. The number of young ranges from two to four. There may be loss of potential young prior to implantation or after implantation. Females apparently do not become pregnant during their first summer.

Males.—The baculum of adult males is between 80 and 90 mm. in length (Pl. II). It is nearly straight but the distal end may be bent dorsally 15 or 20 degrees at about one-third of the way from the tip. The bone is round or oval in cross section and the base is enlarged somewhat. If viewed from the anterior end the tip is seen to be expanded into a three pronged inverted Y. In animals judged to be immature the bone is less massive and the basal end less well developed. Seven bacula from animals thought to be adults weighed from 1780 mg. to 2940 mg. and averaged 2338 mg., while 13 bacula from immature animals weighed from 653 to 1458 mg. and averaged 1134 mg. One baculum of the adult type had the tip cut off and was therefore not weighed. The baculum from a half-grown young obtained on July 22 weighed only 462 mg.

It is well known from the work of Deanesly (1935), Elder (1951) and Wright (1947) that the baculum of mustelids develops to full size only after the animal has reached sexual maturity, and Wright (1950) has shown that in *Mustela frenata* the presence of male hormone is necessary for maturation of the baculum. Accordingly those wolverines with small bacula are judged to be sexually immature.

The testes and epididymides of six adult and ten immature males taken during the fall, winter and early spring months were undeveloped and aspermatic (Table 3). Unmistakable evidence of sexual activity was seen in only four animals. An adult taken on February 4 with testes weighing 8640 mg. showed sperm production in the testis, but no sperm had reached the epididymis. An adult taken on April 4 with testes weighing 14,070 mg. was in active spermatogensis and sperm were present in the tail of the epididymis. Two males considered immature on the basis of their bacula, taken on March 31 and April 4 were apparently just becoming active. A few sperm were in the testes but none in the epididymides. Probably full sexual activity would be found in adult males obtained in late spring or early summer. It is obvious that, since all males killed during November, December and January were without sperm, a winter breeding season can not occur in this species. At the time of implantation the males were sexually quiescent.

Skulls.—The juvenile male taken on July 22, thus about four months old, had almost the entire lacteal dentition in place. All of the sutures were still open but the skull was already as large in several measurements as that of an adult female. The remaining skulls all came from animals taken in October or later and were thus from animals at least six months old. All of these skulls show the

TABLE 4.—*Means of cranial measurements of wolverines*

Number and classification	Greatest length of skull	Condylobasal length	Zygomatic breadth	Post-orbital processes	Post-orbital constriction	Length of sagittal crest
7 ad. males	161.6	146.8	106.1	48.7	34.1	76.3
13 im. males	157.7	146.1	104.0	47.9	35.2	68.9
7 ad. females	147.8	135.8	97.8	46.5	33.4	62.4
3 im. females	144.1	134.9	94.4	43.4	33.4	55.0

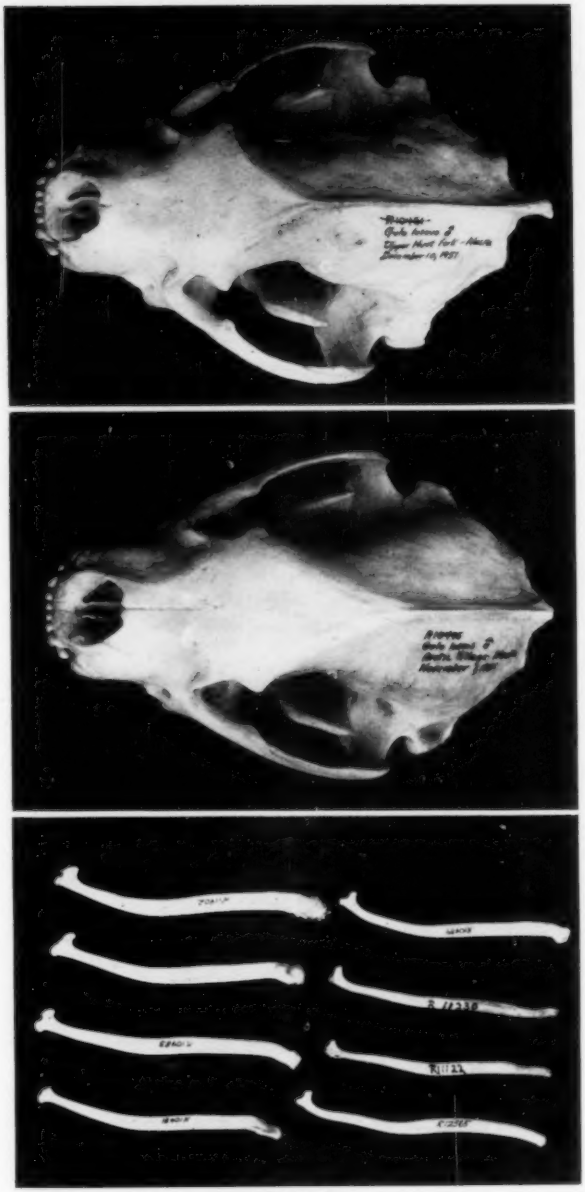

PLATE II

UPPER: Skull of adult male wolverine showing that all sutures have disappeared. The caudal extension of the sagittal crest is clearly shown. About ½ natural size. MIDDLE: Skull of immature male wolverine showing the internasal, naso-maxillary, the naso-frontal and the malar-temporal sutures still open. The sagittal crest is less well developed than in the adult male. About ½ natural size. LOWER: Bacula of adult males on the left and immature males on the right. About ½ natural size.

great majority of the sutures to have disappeared, the permanent dentition is present and in males the sagittal crest is well developed (Plate II). Other writers such as Coues (1877) and Grinnell, Dixon and Linsdale (1937) have remarked about the rapid maturity of the skull in this species.

Means of measurements of the skulls were summarized according to sex and age in Table 4, the immatures separated from the adults on the basis of the reproductive tracts. No one of the cranial measurements taken seems to be critical alone in distinguishing adults from immatures. It would appear that the longer sagittal crest in adult males might distinguish them from the immatures but the *t* test shows this difference is not significant. In adult males the sagittal crest seems to extend posteriorly further than in the immatures. A measurement of this character can be obtained indirectly by subtracting the condylobasal length from the greatest length of the skull. In seven adult males this averaged 14.9 mm. and in twelve immature males it is 11.6 mm. Although there is some overlap in individual cases, when analyzed by the *t* test the difference was found to be significant at the 5 per cent level suggesting that this is a real difference. The same situation is probably true in the females but the number of skulls is not large enough to permit the use of tests of significance.

All of the animals judged to be adults have all of the usual sutures closed. All the immatures taken in the fall and early winter have the malar-temporal, the internasal, and the naso-maxillary sutures still open. Some of the males with small bacula taken in March and April and thus judged to be about one year old have some or all of these sutures closed.

The degree of tooth wear does not seem to be of great significance in estimating age, especially since animals of both classes may show broken teeth partly caused by fighting the trap.

A ratio of eight adult males to 13 immature males was obtained and of seven adult females to only four immature females. In view of these different ratios of young to adults in the two sexes, one might ask if there were reason to suppose that the female wolverine matures a year earlier than does the male. A comparison of these ratios by the chi-square method indicates that there is no reason to suspect this since the calculated value of chi-square is not significant and ratios of eight to 13 and seven to four could be drawn from the same population with considerable frequency. Also the fact that only one type of skull appears in winter-killed immatures suggests rather strongly that there is only one age class of immature animals represented in this sample. It would logically follow that animals of both sexes mature during their second summer.

SUMMARY

The reproductive tracts of 22 male and 11 female wolverines taken mostly during the fall, winter, and early spring months in northern Alaska have been studied. Adult females taken in October, November, and January showed unimplanted blastocysts in their uteri and inactive corpora lutea in their ovaries. Ten blastocysts ranging in number from two to four per female were recovered. The blastocysts may have several hundred cells and they are about 2 mm. in diam-

eter. A late-January and an early-February specimen had implanted embryos of 22 and 68 mm. crown-rump length respectively. Two early-April specimens were lactating but not pregnant. Four females were immature. The wolverine has a long period of gestation like many of the other mustelids. The breeding season is not precisely known but it probably occurs in mid-summer.

The baculum of the male is described. Immature males may be distinguished from adult males by their smaller bacula. The testes of males of both ages were largely inactive during the winter months. Full sexual activity was seen in only one male taken in early April.

The skull of the wolverine matures rapidly, but the young during the first year tend to show open sutures in the facial and zygomatic regions. The sagittal crests of first year animals do not extend as far posteriorly as do those of adults.

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SEX DIMORPHISM IN THE PELVIS OF RODENTS

By William W. Dunmire

Although it has been known for some time that intraspecific structural variation in the region of the pelvis occurs in certain mammals, it was not until 1936 that single pelvis bone shape differences were described and attributed to sex dimorphism (Gardner, 1936). More recent studies on the meadow mouse *Microtus* have demonstrated that the pubic arm of the pelvis in female *Microtus* tends to be narrower than that of the male and that it tends to be longer in proportion to the ischial arm in the female than in the male (Guilday, 1951). Other studies have shown that sex differences are present in the pelvis of *Apodemus*, *Mus*, and *Clethrionomys* and that males may be separated from females quite accurately in these species by taking certain pelvic measurements (Becker, 1954).

Use of a single innominate bone only for sexing (and perhaps aging) small rodents may prove a useful device for the worker in population dynamics. Knowledge of pelvic sex dimorphism finds immediate use in owl pellet analysis since pelvis halves of small rodents are usually found nearly intact in the pellet. The technique proved valuable in a recent study of the relation between snowy owl predation and the lemming cycle in Alaska.

Method.—Measurements were made on the pelves of seven species of rodents. In each species the length of the pelvis was measured since there is good indication that pelvis length is correlated with sexual maturity. Other measurements were chosen that would bring out the differences between the male and female pelvis in each species. To avoid bias in taking the measurements, the sex of each specimen was not determined (from labels) until after the dimensions were recorded. Dial calipers were used, and the measurements were made to the nearest tenth of a millimeter.

Some of the lemmings examined were obtained near Barrow, Alaska, with assistance from the Office of Naval Research (Contract N7 ONR-29542 with the University of California) in 1951 and 1952. For permission to examine other lemmings from the collection of the University of Kansas I am grateful to Dr. E. R. Hall. All other specimens examined are in the Museum of Vertebrate Zoology at the University of California.

FAMILY CRICETIDAE

Microtus californicus (subspecies *californicus* and *eximius*).—Sixty-two *Microtus* pelves (29 ♂♂ : 33 ♀♀) were examined. The sex differences in the pelvis of *Microtus* have already been outlined. In order to show the differences in the pubic arm elongation, two measurements were made; *a*—from the posterior angle of the ischium to the nearest edge of the acetabulum, and *b*—from the ventral apex of the pubis (i.e., the pubic symphysis) to the nearest edge of the acetabulum. The ratio of measurement *b* to measurement *a* (b/a) is used as an index. Another measurement, *p*—the thinnest width of the pubis, was taken (Fig. 1). By plotting *p* against b/a (Fig. 2, Graph 1), males are clearly separated from females except in one case. The single male pelvis that falls into the female

TABLE 1.—*Ranges and means of pelvis measurements, and formulae for separation of male from female pelves*

Graph no.	Species	Formula for separation	Males		Females	
			Range	Mean	Range	Mean
1	*Microtus californicus*	$y = 1.05x - .76$	b/a: 1.10 –1.46	1.270	b/a: 1.28–1.70	1.438
			p: 0.5 –1.5	1.059	p: 0.3 –0.7	0.545
2	*Lemmus trimucronatus*	$y = 5.4x - 6.60$	b/a: 1.17 –1.47	1.334	b/a: 1.36–1.70	1.541
			p: 1.0 –1.6	1.332	p: 0.5 –1.4	0.914
3	*Peromyscus maniculatus*	$y = 1.37x - 1.29$	b/a: 1.18 –1.38	1.276	b/a: 1.31–1.58	1.452
			p: 0.5 –0.9	0.677	p: 0.4 –0.6	0.482
4	*Neotoma fuscipes*	$y = 2.5x - 1.79$	b/a: 1.15 –1.36	1.243	b/a: 1.21–1.42	1.354
			p: 1.2 –1.8	1.580	p: 1.0 –1.5	1.150
5	*Dipodomys heermanni*	$y = 6.38x - 7.02$	b/a: 1.05 –1.20	1.113	b/a: 1.14–1.28	1.208
			t: 0.2 –1.4	0.752	t: 0.2 –0.5	0.272
6	*Citellus beecheyi*	$y = 7.14x - 0.05$	c/d: .149– .282	0.209	c/d: .174–.421	0.294
			t: 1.1 –3.2	2.196	t: 1.0 –1.8	1.513

area on the graph is 19.2 mm. long, probably the pelvis of an immature mouse. Reliability of diagnosis is probably low for pelves shorter than 20.0 mm.

Lemmus trimucronatus alascensis.—Forty-eight pelves (19♂♂:29 ♀♀) were examined. The pelvis sex differences were found to be the same as in the other microtine species, and therefore the same measurements were taken. Graph 2 of Figure 2 summarizes the findings. In both microtines (*Lemmus* and *Microtus*) it was found that the posterior margin of the ischium tends to be concave in the female and convex in the male. This enables a sex determination to be made easily from inspection. Thirty-seven *Lemmus* pelves were sexed by gross examination, and all but one were identified correctly. Reliability is probably low for pelves shorter than 20.0 mm.

Peromyscus maniculatus sonoriensis.—Sixty-four pelves (36 ♂♂:28 ♀♀) were examined. Graph 3 of Figure 2 summarizes the findings. Here it is seen that no sex overlap is present in the specimens examined; however, reliability is probably low for pelves shorter than 16.0 mm.

Neotoma fuscipes (subspecies *annectens*, *monochroura*, and *streatoris*).—Forty pelvis specimens were analyzed (20 ♂♂:20 ♀♀). As in the other three cricetid

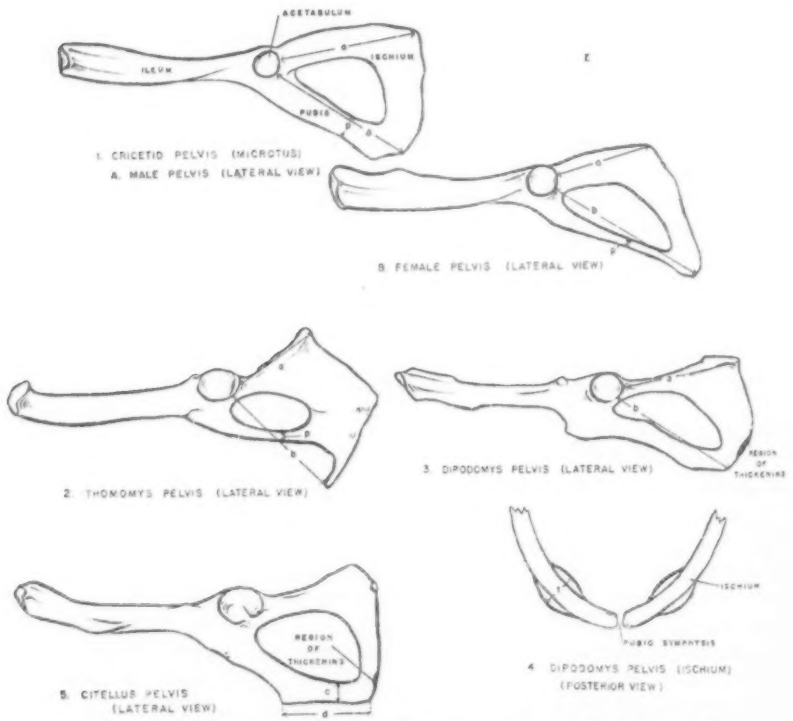

FIG. 1.—Sex dimorphism in the pelvis of rodents. See text for explanation.

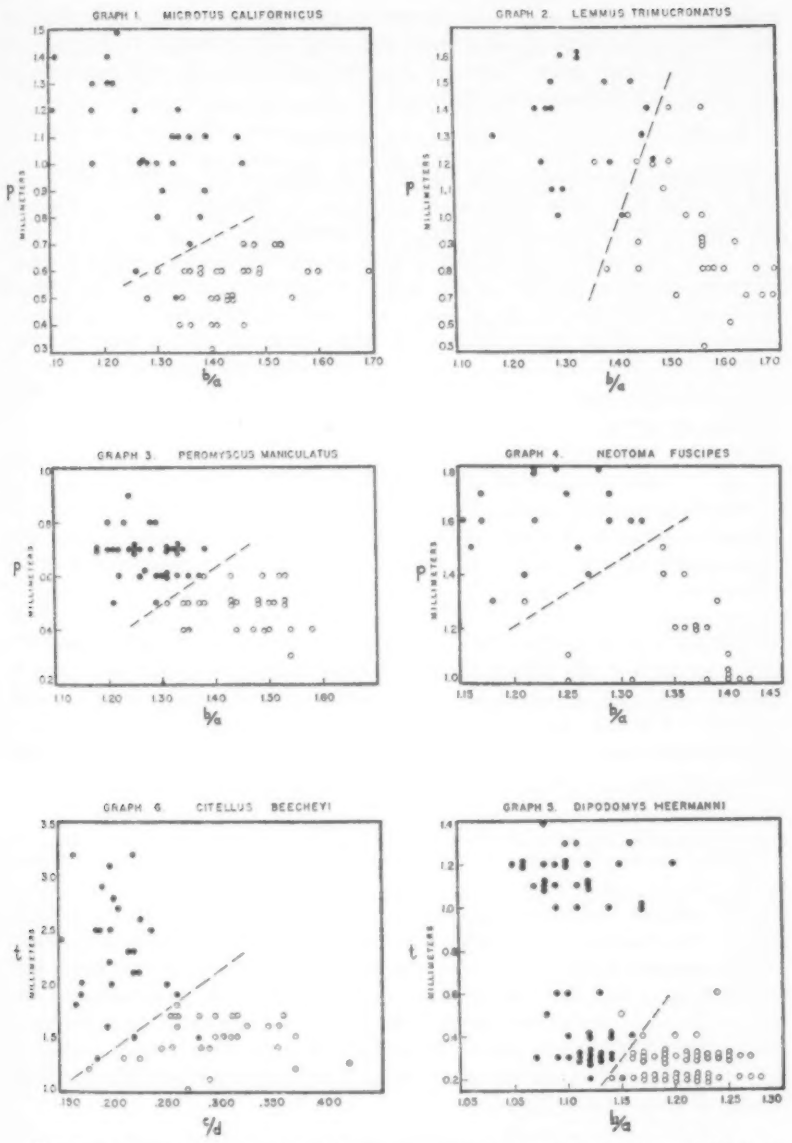

FIG. 2.—Separation of sexes by pelvis measurements in six kinds of rodents. Solid circles represent males, open circles, females. For summarization of the range and mean of measurements of males and females, and for formulae of the lines separating males from females see Table 1.

rodents, pubic width and pubic elongation were the critical sex differences in the pelvis, so the same measurements were used (Fig. 2, Graph 4). Sex overlap occurred in a single pelvis.Those pelves shorter than 36.0 mm. were not included since reliability of diagnosis is low for them.

FAMILY GEOMYIDAE

Thomomys bottae (subspecies *albatus* and *bottae*).—Thirty-seven specimens (19 ♂♂:18 ♀♀) were studied. The shape of a *Thomomys* pelvis is different from that of the cricetid rodents (Fig. 1). Although the pubis tends to be thinner and more elongated in the female *Thomomys*, there is a great deal of overlap between males and females. In this species the posterior portion of the ischium also tends to be thinner in the female, and another measurement, *e*, was made of the thinnest width of the ischium in this area. These differences, however, were likewise inconsistent. No set of measurements was found that would separate male from female pelves with accuracy. Parous females can, of course, be identified by the interpubic separation of the two innominate halves in intact specimens.

FAMILY HETEROMYIDAE

Dipodomys heermanni saxatilis.—One hundred and ten kangaroo rats (56 ♂♂:54 ♀♀) were examined for pelvic differences. Pubic elongation was again characteristic of the females, but pubic width did not appear to have sexual differences. However, in males there tended to be a bony swelling on the posterior margin in the ventral region of the ischium, and measurement *t* was made of this (Fig. 1). It was noted that this swelling was present only in the males with a longer pelvis, and the thickening may well be due to increased pelvic muscle activity resulting in the need for larger attachments for sexually mature males. Graph 5 of Figure 2 plots the thickening against the pubic elongation ratio, and little overlap of sexes is observed. Pelves shorter than 25.0 mm. are not included since reliability for these lengths is low.

FAMILY SCIURIDAE

Citellus beecheyi (subspecies *beecheyi*, *parvulus*, and *douglasi*).—Fifty-nine pelves (29 ♂♂:30 ♀♀) were examined. Here it was noticed that, as in *Dipodomys*, males tended to have an ischial thickening. Also the pubic symphysis tended to be shorter but the pubis wider in the females than in the males (Fig. 1). Measurement *d* was made on the (ventral) length of the pubic symphysis, and measurement *c* was made of the pubis width (thinnest) at the symphysis. The ratio of *c* to *d* (*c*/*d*) was used as an index to demonstrate the differences in the pubic region. Plotting *c*/*d* against *t* separates most males from females, and when only specimens with a pelvis longer than 39.0 mm. are considered, there is little overlap of sexes (Fig. 2, Graph 6).

DISCUSSION

It has been shown that measurable differences in the shape of the innominate bone exist between male and female specimens of the seven species of rodents

that were examined, and that in all the rodents studied except *Thomomys* males can be distinguished from females with a fairly high assurance of accuracy. The region of sex overlap in all cases tended to consist of specimens that had the shorter pelves, and these are assumed to be from the youngest animals. When sexing rodents by pelvis shape, therefore, a pelvis length minimum should be set below which the specimen will not be considered.

Subspecific differences in pelvis shape are so small that apparently they are of little importance. In the present study two subspecies of *Microtus californicus*, three of *Neotoma fuscipes*, and three of *Citellus beecheyi* were used, yet there was no indication of subspecific difference in pelvis shape within the species. Age (reflected in pelvis length) rather than race seems to be a more important factor.

In certain female rodents a separation of the pubes (i.e. the pubic symphysis region) occurs during gestation and is directly caused by sex hormones (Hall, 1947; Hall and Newton, 1946). This interpubic separation is characteristic of all the forms studied here except *Citellus*. The pelvic shape differences in the other six species might well be due to modifications of the female pelvis to facilitate the separation. Preliminary experiments on *Microtus* indicate that estrogen and testosterone have an effect on the pelvis shape of immature mice.

It is hoped that the graphs and formulae presented above will be useful to others attempting to determine the sex of these species from skeletal material, and that the technique will be applied by others to additional kinds of mammals.

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HEMATOLOGICAL STUDIES ON MAMMALS FROM ALASKA

By X. J. Musacchia, C. G. Wilber, and T. W. Gorski

It is evident, according to Downey (1938), that hematological studies on mammals other than the common laboratory and domestic forms are relatively scarce. The comprehensive tabulations in the appendix of Wintrobe's (1953) work on hematology show the dearth of information in this field.

During the course of a research problem dealing with the physiology of arctic animals, considerable hematological data were obtained from a variety of mammalian specimens. The work of Slane and Wilber (1952) on the hematology of the red backed mouse, *Clethrionomys dawsoni* from central Alaska, is the only recent contribution to our knowledge of blood cells in wild Alaskan mammals. In order to keep interested investigators informed, this report on blood counts, differentials and erythrocyte measurements from a number of mammals collected in Alaska is presented.

Species.—The following species were studied in this investigation: Hudson Bay ground squirrel, *Citellus parryii parryii*; Yukon ground squirrel, *Citellus osgoodi*; Alaska red squirrel, *Sciurus hudsonicus petulans*; MacFarlane meadow mouse, *Microtus macfarlani*; black bear, *Ursus americanus*; ochraceous woodchuck, *Marmota monax ochracea*; snowshoe hare, *Lepus americanus*; cottontail rabbit, *Sylvilagus sp.*; Richardson weasel, *Mustela erminea richardsonii*; northwestern muskrat, *Ondatra zibethica spatulata*; Alaska porcupine, *Erethizon epixanthum myops.*

Field and laboratory work.—During the summer of 1951, red squirrels, meadow mice, woodchucks, snowshoe hares and muskrats were collected at various places in central Alaska. Some ground squirrels, porcupines, weasels, rabbits and the black bear were supplied from the menagerie at the Arctic Aeromedical Laboratory, Ladd Air Force Base, Fairbanks, Alaska.

Blood samples for counts and differentials were generally taken by bleeding an animal from a digit. The blood smears were stained with Wright's or Giemsa's technique. Erythrocyte measurements were made using a calibrated ocular micrometer.

This research project was supported in part by the United States Air Force, Contract Number AF 33(038)-30103.

Results and discussion.—Details of the erythrocyte counts are given in Table 1. In general, the red blood cell counts of the Alaskan rodents studied do not differ from those of other rodents as published (Table 2).

The red blood cell counts from four newborn *Sciurus* are considerably less than those from the six juveniles (Table 1). This observation is in keeping with similar findings in common laboratory animals, rabbit, rat, and dog (Scarborough, 1930–1931, *a*, *c*, *d*; and Morris, *et al.*, 1939).

Among the various animals studied the means of the erythrocyte diameters differ: the marmot has the largest erythrocyte, 8.19 micra; the porcupine, 7.84 micra; the rabbit and the hare, 6.95 and 6.89 micra respectively; the squirrels range from 6.66 to 7.15 micra; the mouse and the weasel have the smallest

TABLE 1.—*Blood counts, differentials and sizes of erythrocytes in Alaskan mammals*

	Erythrocytes		Leucocytes					
	RBC/mm.³	Diameter in micra	WBC/mm.³	Differential				
				N	E	B	L	M
	Citellus parryii parryii							
1	6,095,000	7.23	11,320	73.0	0.8	2.3	20.8	2.6
2	—	7.00	—	79.6	1.0	0.0	18.6	0.7
3	—	7.00	—	64.0	1.0	1.0	33.0	1.3
4	—	7.21	—	57.0	3.0	0.0	35.0	5.0
5	—	6.86	—	—	—	—	—	—
6	—	7.14	—	—	—	—	—	—
7	9,575,000	7.35	5,840	63.0	3.0	0.3	32.6	1.0
8	6,970,000	7.21	7,440	81.5	2.0	0.5	15.5	0.5
9	7,390,000	6.93	5,640	81.0	1.0	0.5	16.5	1.0
10	8,750,000	7.56	3,300	70.5	4.0	0.0	25.0	0.5
11	6,505,000	7.49	2,720	76.5	1.5	0.0	21.5	0.5
12	8,565,000	7.42	20,180	88.5	1.0	1.0	8.5	1.0
13	7,225,000	7.14	5,620	88.0	0.5	0.0	10.5	1.0
14	7,230,000	6.58	21,340	81.5	2.5	0.5	15.0	0.5
15	6,875,000	6.86	17,920	72.5	1.0	0.0	25.0	1.5
16	6,610,000	7.47	33,560	91.5	0.5	0.5	7.0	0.5
17	6,670,000	7.42	13,520	84.5	1.5	0.5	13.5	0.0
18	7,420,000	7.00	21,620	90.5	0.5	0.0	7.0	2.0
19	10,120,000	—	9,090	—	—	—	—	—
Mean	7,564,000	7.05	12,794	77.6	1.7	0.4	19.1	1.2
	Citellus oxgoodi							
1	—	7.46	—	66.5	0.5	0.5	30.0	3.0
2	—	6.53	—	74.5	4.2	1.2	17.6	2.5
3	—	7.93	—	69.0	2.0	4.3	20.3	4.0
4	—	7.70	—	43.0	4.0	3.0	49.0	1.0
5	—	7.23	—	44.6	1.8	4.4	45.0	4.4
6	—	6.53	—	66.6	2.0	1.6	29.0	1.0
7	9,320,000	6.79	10,940	57.0	4.0	0.7	34.3	4.0
8	8,015,000	6.65	11,860	74.0	3.6	0.0	22.0	0.3
9	8,095,000	7.49	9,940	53.0	9.0	0.3	36.3	1.3
10	7,890,000	7.21	10,540	55.6	5.0	0.3	37.0	2.0
Mean	8,330,000	7.15	10,820	60.4	3.6	1.6	32.5	2.5
	Sciurus hudsonicus petulans							
(adults)								
1	—	7.00	—	81.3	0.0	0.0	18.0	0.7
2	—	6.37	—	26.3	0.3	0.7	71.0	1.6
3	—	6.30	—	46.6	0.7	0.0	51.6	1.0
4	—	6.72	—	21.6	1.0	0.3	75.3	1.6
5	—	6.93	—	—	—	—	—	—
Mean	—	6.66	—	48.9	0.5	0.3	53.9	1.2

TABLE 1.—(*Continued*)

	Erythrocytes		Leucocytes					
	RBC/mm.³	Diameter in micra	WBC/mm.³	Differential				
				N	E	B	L	M
(juveniles)								
6	7,245,000	6.37	500	32.7	0.0	1.0	64.0	2.1
7	8,535,000	6.93	440	18.0	0.0	0.7	78.5	2.5
8	7,145,000	6.93	—	—	—	—	—	—
9	7,485,000	7.14	870	—	—	—	—	—
10	7,625,000	6.72	—	—	—	—	—	—
11	7,290,000	7.07	1,280	—	—	—	—	—
Mean	7,554,000	6.86	773	25.3	0.0	0.9	71.3	2.3
(newborns)								
12	—	6.93	—	—	—	—	—	—
13	4,208,000	7.91	—	3.0	0.0	0.0	91.0	6.0
14	2,460,000	7.84	—	—	—	—	—	—
15	4,463,000	—	—	—	—	—	—	—
16	4,075,000	—	—	—	—	—	—	—
Mean	3,802,000	7.56	—	3.0	0.0	0.0	91.0	6.0
Microtus macfarlani								
1	—	6.30	—	10.4	0.4	0.4	86.6	2.2
2	—	5.88	—	—	—	—	—	—
3	—	5.95	—	7.0	0.2	0.2	91.0	0.2
4	—	6.02	—	13.6	6.6	1.2	77.8	0.8
5	—	6.79	—	8.0	0.5	2.5	86.0	3.0
Mean	—	6.19	—	9.9	1.9	1.1	85.4	1.6
Lepus americanus								
1	—	7.00	—	12.8	1.8	6.0	75.3	3.5
2	—	7.00	—	20.5	2.3	7.7	56.3	13.1
3	—	6.86	—	48.8	0.2	3.3	38.1	9.5
4	—	6.93	—	18.0	0.6	0.8	73.4	7.4
Mean	—	6.95	—	25.0	1.2	4.4	60.8	8.4
Erethizon epixanthum myops								
1	—	7.98	—	48.5	0.0	0.6	48.3	3.0
2	—	7.63	—	42.8	1.0	0.0	54.6	1.6
3	—	7.63	—	39.0	0.2	0.2	58.8	1.4
4	—	8.12	—	22.4	0.2	0.5	74.4	2.8
Mean	—	7.84	—	38.2	0.4	0.3	59.0	2.2
Sylvilagus sp.								
1	—	7.07	—	24.8	2.0	0.8	65.0	7.4
2	—	6.72	—	69.6	1.0	0.8	24.2	4.4
Mean	—	6.89	—	47.2	1.5	0.8	44.6	5.9

TABLE 1.—(*Concluded*)

	Erythrocytes		Leucocytes					
	RBC/mm.³	Diameter in micra	WBC/mm.³	Differential				
				N	E	B	L	M
Mustela erminea richardsonii								
1	—	6.30	—	43.6	5.9	4.7	39.4	0.9
2	—	6.40	—	45.0	2.4	6.7	42.4	3.3
Mean	—	6.35	—	44.3	4.2	5.7	40.9	2.1
Marmota monax ochraceous								
1	—	8.19	—	33.0	25.1	0.4	32.3	9.3
Ondatra zibethicus spatulata								
1	—	—	—	33.9	6.4	0.5	55.4	4.5
Ursus americanus								
1	—	—	—	75.6	0.0	1.8	22.2	0.0

erythrocytes, 6.19 and 6.4 micra respectively. The values obtained compare closely with those recorded by Scarborough (1930–1931*a*, *b*, *c*, *d*) for other related mammals: rabbit, 6.7 micra (average from 8 authors); rat, 6.13 micra (average from 7 authors); dog, 6 to 8 micra (average 20 authors).

It is interesting to note that among the species studied the larger species have the largest red cells: *Erethizon*, 7.84 micra; *Marmota*, 8.19 micra; *Lepus*, 6.95 micra; *Sylvilagus*, 6.89 micra. Conversely, the smaller species have the smallest red cells: *Mustela*, 6.35 micra; *Microtus*, 6.19 micra. Such correlations have often been made in the past. Gulliver's (1875) work is one of the earlier and more outstanding investigations. He showed that often within a given mammalian order, direct relationship exists between the size of the erythrocyte and the animal size.

The erythrocytes of *Microtus* are primarily monochromatic; however, polychromatic cells were quite common. Slane and Wilber (1953) reported that *Clethrionomys* has "large numbers of polychromatic red cells" and Scarborough (1930–1931,*b*, *c*) reported that polychromatophilia is common in the guinea pig

TABLE 2.—*Red blood cells in millions per mm.³ in various rodents*

Animals	RBC's	Source
Hudson Bay ground squirrel	7.5	Present work
Yukon ground squirrel	8.3	Present work
Alaskan red squirrel (juveniles)	7.6	Present work
White rat	6.6	Wintrobe, Shumacker and Schmidt (1936)
White mouse	7.8 to 9.7	Petri (1935)
Woodchuck	7.3	Jordan (1938)
Guinea Pig	6.4	Drastisch (1928)

and the rat. With such widespread reports of polychromatophilia among the Rodentia it is reasonable to consider that this may be a characteristic of this phylogenetic group, and further investigation is therefore indicated.

Many mammals show evidence of wide variation in total number of leucocytes per mm³. of blood: cat, 9,200 to 24,000 (Vaulont, 1935); dog, 8,000 ± 5,000; horse, 6,000 to 12,000; and rat, 8,000 to 15,000 (Scarborough, 1930–1931*c*, *d*, *e*). Adult specimens of the squirrel, *Citellus parryii parryii*, also have a wide range: 5,620 to 21,620. The range is not so great in *Citellus osgoodi*, 9,940 to 11,860 WBC/mm³. The low leucocyte counts in the juvenile specimens of *Sciurus hudsonicus petulans* cannot be explained at this time.

In the differential studies of *Citellus parryii parryii* the neutrophils and lymphocytes are in greatest proportion, 78 per cent and 19 per cent respectively; the basophils are relatively scarce, less than 1 per cent; monocytes and eosinophils are between 1 and 2 per cent. In *Citellus osgoodi* neutrophils and lymphocytes are also in greatest proportions, 60.4 per cent and 32.5 per cent respectively; eosinophils, basophils and monocytes are generally in equal proportion. There is therefore a similarity in the differentials of the two representatives of the genus *Citellus*. Their leucocytes occur in the following descending order: neutrophils, lymphocytes, eosinophils, monocytes, and basophils. Jordan (1938) found similar leucocyte proportions in another wild rodent, the woodchuck. The differential of the red squirrel studied is notably different from that of the ground squirrel in two respects, namely, that the red squirrels have high percentages of lymphocytes and low percentages of neutrophils. Furthermore a relationship with age appears to exist. The older animals have greater numbers of neutrophils and less lymphocytes as compared with the younger specimens.

It is noteworthy that both wild and laboratory species of mice have some similar leucocyte characteristics. The lymphocytes are the predominant leucocyte: laboratory mouse, *Mus*, 67.8 per cent (Scarborough 1930–1931*c*); red backed mouse, *Clethrionomys*, 70.7 per cent ± 13.3 (Slane and Wilber 1952); meadow mouse, *Microtus*, 85.4 per cent (present study). The basophilic granulocytes make up about 1 per cent of the total leucocytes in *Microtus*, and *Clethrionomys* was reported lacking in basophils. Neutrophils average about 10 per cent of the leucocytes of *Microtus*. This value is much lower than earlier reports for other mice: *Mus*, 23 per cent (Simonds, 1925); *Mus*, 8 per cent to 45.5 per cent (Downey, 1938); *Clethrionomys*, 22.5 per cent (Slane and Wilber, 1952). It is evident, therefore, that (1) *Microtus* has relatively less neutrophils than other mice and (2) considerable variation exists in the reported numbers of neutrophils in various species of mice.

The differential studies of the rabbit, *Sylvilagus*, and the hare, *Lepus*, show that some differences exist in these two animals (Table 1). However, differential results of both animals fall within the range given by Scarborough (1930–1931*a*) for the common laboratory rabbit (*Oryctolagus*): polymorphonuclears, 43.4 per cent (30–50); lymphocytes, 41.8 per cent (30–50); large mononuclears and transitionals, 9.0 per cent (2–16); eosinophils, 2.0 per cent (0.5–5); and basophils, 4.3 per cent (2–8).

The woodchuck, *Marmota*, showed a definite eosinophilia (25% eosinophils). The cause for this condition was not determined. The reported eosinophil value for woodchuck is 1.7 per cent (Jordon, 1938); for other rodents, guinea pig, 4.8 per cent (Scarborough 1930–1931*b*); and hamster, 0.7 per cent (Steward, *et al.*, 1944). It is possible that the specimen examined was parasitized or infected and as a result showed the eosinophilia.

The muskrat, *Ondatra*, has the following unique leucocytic characteristics: the eosinophil nuclei are practically all "doughnut" shaped, in contrast to the usual bilobed or polymorphonuclear conditions common to mammals; the acidophilic granules are extremely fine as compared with the more coarse granulation seen in many other mammals. A more detailed study of these characteristics is in progress.

SUMMARY

Some hematological studies were made of mammals from Alaska. Squirrel red cell counts were similar to those of other members of the Rodentia. The wide variation in white cell counts of squirrels is a common characteristic of many mammals. Hematological differences related to maturity occur in *Sciurus*. The range of erythrocyte diameter in all species studied is comparable to those already reported for mammalian fauna and a direct relationship between red blood cell size and animal size was shown. Differential studies corroborate the established fact that a wide variation in the percentage of leucocyte types exists in mammals. The suggestion is made that polychromatophilia is a characteristic of wild and common laboratory animals of the order Rodentia.

In general, the blood picture of wild Alaskan mammalian fauna is not exceptionally different from the hematological studies reported for other related forms.

Addendum.—Sometime after this paper had been in press, a study of the blood of *Citellus parryi* Sabine was reported (Lieb and Wilber, 1954). Their differentials are somewhat at variance with those herein reported for *Citellus*. The method of obtaining blood differs considerably between these two studies and may offer some explanation for the differences in leucocyte percentages.

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AN ELEVEN YEAR HISTORY OF A SIGMODON POPULATION

BY EUGENE P. ODUM

While general observation has indicated that annual fluctuations in population density of rodents in southern United States are less "cyclic," i.e., peaks less regular, than is the case in the classic northern four-year cycles, few long-term observations have been made on populations in stable habitats. The possibility of a north-south difference in the nature of population oscillations has an important bearing on current theories of "cycles." For the past eleven years trapping has been carried out according to a consistent plan in an old field where habitat features have been relatively constant. The field is located near Athens, Clarke County, Georgia in the Piedmont section of the state. The cotton rat, *Sigmodon hispidus*, comprised the great bulk of the readily trappable small mammal population in the old field, which is in a stage of vegetative succession favorable to the species. (Cotton rats occurring in Georgia except for the coastal strip, below 100 foot contour line, have been assigned to the subspecies *Sigmodon hispidus komareki* by Gardner, 1948.) Results of this study are presented simply as evidence of changes in density, natality, age distribution and other population characteristics that apparently have occurred on a limited area. No attempt will be made at this time to interpret these data in terms of various theories that have been advanced to explain population cycles.

The writer is indebted to the following students and former students who helped with trap setting and specimen preparation at various times during the period: Drs. Robert A. Norris and David W. Johnston, James C. Major, H. C. Robert, James O. Harrison, Edward J. Kuenzler, Jack Lowe, and J. B. Gentry.

The study area.—The old field selected for this study (Pl. I) is one of a series

of abandoned fields lying on a slope a quarter of a mile east of the North Oconee River at a point opposite the Dairy Farm of the University of Georgia, which lies on the west side of the river. The fields are typical of abandoned cotton lands of the Piedmont region. At the start of the study the field had been abandoned about eight years and was in the broomsedge-shrub (*Andropogon-Rubus*) stage of succession. Both gully and sheet erosion are evident throughout the area. Terraces constructed along contours during previous cultivation remain prominent and are an important habitat feature. The particular field was selected because both previous erosion and the absence of a nearby source of pine seeds would operate to keep the field in virtually the same stage of succession for many years. Except for continued growth of small trees and shrubs already present, especially on the old terraces, and the invasion of a few new pine seedlings, the area has remained remarkably stable. The last peak in cotton rat abundance in 1952–3 was about the same order of magnitude as the first peak observed in 1946 (Fig. 1), which would indicate that the carrying capacity of the area for cotton rats has indeed remained about the same over the eleven year period.

Broomsedge, *Andropogon virginicus*, forms an almost continuous cover over the area (Pl. I) except for a few very badly eroded spots which have remained bare. Old field forbs such as species of *Gnaphalium*, *Solidago*, *Lespedeza*, and

PLATE I

The study area as it appeared in the early spring of 1952. The white flag marks the beginning of trapline no. 1, which continues over the hill in the background. Line no. 2 is to the right just out of the picture. The first row of trees and shrubs (in the foreground) marks the first low terrace (see Fig. 3). A second and larger terrace is mostly out of view over the hill, but a portion of it may be seen in the left background. The light-colored stems in the foreground are broomsedge (*Andropogon*) and the dark stems are canes of blackberries (*Rubus*).

Aster are secondary seasonal dominants. Scattered throughout the grass are numerous small and a few large clumps of blackberry (*Rubus*) and greenbrier (*Smilax*). There are a few pine seedlings (*Pinus taeda* and *P. echinata*) here and there as well as a few small deciduous trees and shrubs, chiefly persimmon (*Diospyros virginiana*), sumac (*Rhus glabra*), water oak (*Quercus niger*), and plum (*Prunus*). Cover is more dense on the low terraces where the growth of grasses, blackberries, trumpet vines, shrubs and small trees is thicker (Pl. I).

The study area is surrounded by similar fields a few of which have been cultivated more recently, or are mowed for hay. Narrow hedgerows or thickets separate the study area from other fields. Thus, the study area is in contact with other fields where cotton rats are numerous.

Methods.—During the first four years (1944–47) the population was sampled each fall by means of a half-acre quadrat following the method of Bole (1939). When Dr. John B. Calhoun organized the North American Small Mammal Census in 1948 we switched to the use of a double trapline and sampled the population both spring and fall of each year in order that our data might be comparable with that obtained by other workers following Calhoun's plan (Calhoun, 1948). Spring trapping was done during the first two weeks in May and fall trapping between October 20 and November 20. Traplines were run at right angles to terraces as shown in Figure 3. Each line consisted of 20 stations 25 feet apart with three traps (two regular commercial rat traps and one mouse or museum special trap) at each station. The lines were placed 200 feet apart as originally standardized by Calhoun (1948). The two lines contained 40 stations with a total of 120 traps, which were operated for three successive days (totaling 360 trap nights). On one or two occasions heavy rains sprung traps and the line was run for an extra day, in order to obtain three effective 24 hour periods of trapping. During the first four years only number, sex and approximate age of specimens were recorded, but beginning in 1948 all animals were weighed, measured and examined for reproductive condition; some were kept as study skins. The same bait was used throughout, i.e., a half of a large peanut tightly impaled on the trigger release. It was possible to compare the population level on the study field with the general level in the region for some of the years when some other trapping was done in the Athens vicinity. Also, in 1949, a marking-recapture study was carried out on another, similar field. Animals were marked in February, May, August, and November; data on home range and longevity were useful in the interpretation of trapline results. In 1948 Robert Norris and David Johnston set out half-acre quadrats and double traplines in the same area simultaneously. They found that the double trapline caught approximately twice as many animals as the quadrat. On this basis the quadrat data of 1944–47 were converted into trapline density.

Because our studies on home range size in *Sigmodon* are incomplete at this time, trapline animal numbers can not be converted into density in terms of number per acre with any degree of confidence. However, it appears from home range data at hand that for *Sigmodon* the double trapline samples approximately one acre, as is also indicated by the quadrat-trapline comparisons mentioned above.

TABLE 1.—*Numbers of small mammals taken per double trapline in the same field in fall (F) and spring (S) of 1944 through 1954*

Species	1944	1945	1946	1947	1948		1949		1950		1951		1952		1953		1954		Total
	F	F	F	F	S	F	S	F	S	F	S	F	S	F	S	F	S	F	
Sigmodon hispidus	20	10	56	15	6	59	8	29	0	17	0	8	0	51	8	42	2	2	333
Reithrodontomys humulis				1		1				5						1			8
Peromyscus polionotus	2																		2
Cryptotis parva	3			1			1			3						2			10
Microtus pennsylvanicus			2																2
Mus musculus								1		1		1				1			4
Peromyscus nuttalli							1				2								3
Peromyscus leucopus																	1		1

RESULTS

Numerical density.—The total catch is shown in Table 1, and the annual fluctuations are diagramed in Figures 1 and 2. Seven species of small mammals other than cotton rats were taken, but only in small numbers and at irregular intervals. The habitat was somewhat far advanced, succession-wise, to be favorable for *Peromyscus polionotus*, *Cryptotis*, and *Reithrodontomys* while it was too "young" for *P. nuttalli* and *P. leucopus*. *Microtus* is rare in the region and was taken in the study area only in 1946. As shown in Figure 2 there seemed to be a tendency, perhaps only coincidental, for these "marginal" species to invade the field during periods when *Sigmodon* was less common.

As shown in Figure 1, autumn densities of *Sigmodon* oscillated rather sharply between high levels of 50 or more per trapline to less than 20, with a high density occurring in four of the eleven years. There were three major peaks if we consider 1952 and 1953 as one peak. The only year with a fall catch of intermediate size was 1949, and this could well be considered part of the second peak. Thus, it would appear that there have been three well marked "cycles" with major peaks in 1946, 1948, and 1952. The interval between peaks was two and four years. The peaks that occurred on the study area did not always synchronize with those on other local areas, but as nearly as could be determined from somewhat sporadic random trapping in *Sigmodon* habitat, peaks for the Athens region as a whole coincided within a year or so with peaks on the study area.

Spring and fall density since 1948 is compared in Figure 2. In each year, except for 1954, fall density was higher than spring density. While a low density was to be expected in 1954 following two years of abundance, the exceedingly dry sum-

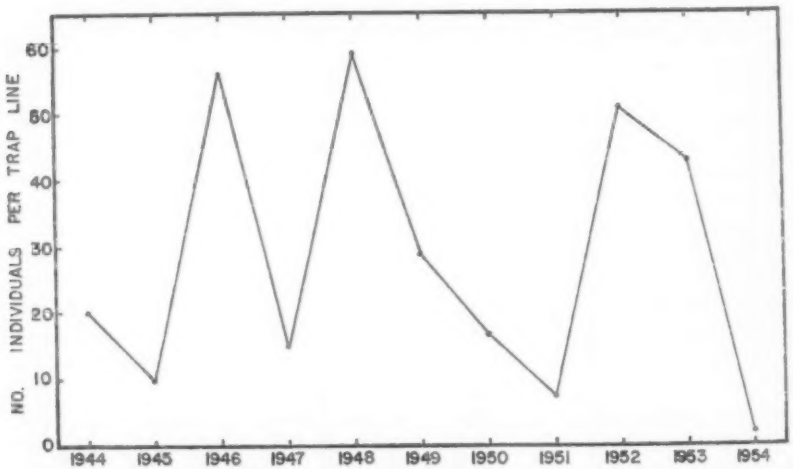

FIG. 1—Autumn (November) densities of *Sigmodon* in number of individuals caught in the double trapline (120 traps in two lines of 20 stations each) between 1948 and 1954 and in equivalent quadrats 1944-1947 (see Table 1).

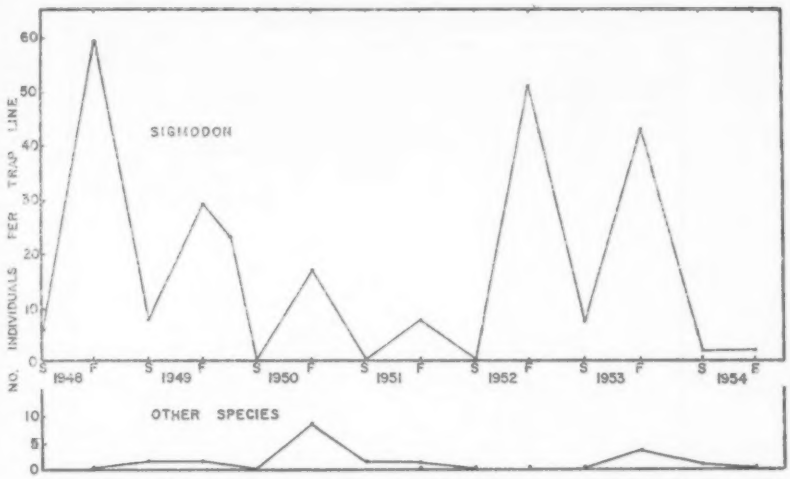

FIG. 2.—Spring (May) and autumn (November) densities in number of individuals caught in the double trapline (see Table 2).

mer and fall of 1954 may have depressed the population so that the usual recovery from the spring low did not occur, at least not by the time of the November trapping period. A seasonal cycle with a low point in the spring and a high point in the fall appears to be the usual rule in northern areas since the major part of the breeding season occurs between these two periods. However, we are finding that the seasonal cycle in *Peromyscus polionotus* on the Coastal Plain is often reversed, with the greatest abundance coming in the late winter or spring and the least abundance in late summer or fall. Pournelle (1952) and McCarley (1954) have reported the same thing for *Peromyscus gossypinus* in Florida and Texas. At present this reversed rhythm is interpreted as due to the depressing effects of hot weather in midsummer, which results in the highest natality occurring in the more favorable periods of late winter and early spring. Since cotton rats breed equally well throughout the year when kept in captivity under constant temperature (Meyer and Meyer, 1944) it would appear that photoperiodicity is not a major regulating factor as is true for some mammal species. Consequently, temperature is undoubtedly important. It is apparent from Figure 2 that, in most years, *Sigmodon* in northern Georgia may be expected to exhibit a "northern type" seasonal cycle of abundance. Since Komarek (1937) has reported that cotton rats in southern Georgia also reach a peak in the fall, it may be that reproduction in this well adapted southern species is not curtailed by high temperatures in summer, as is the case with *P. gossypinus*, but instead reproduction is more likely to be inhibited by low temperatures in winter.

In Figure 3 the total number of cotton rats caught at each of the twenty stations on the two lines is shown in relation to the bushy terraces and the more grassy inter-terrace areas. As might be expected, the catch was greatest in the

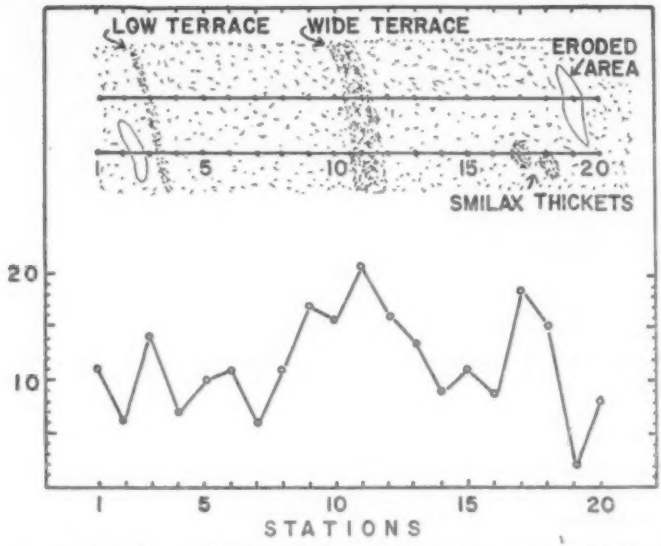

FIG. 3.—Total number of *Sigmodon* caught at each station on the double line between 1948 and 1954 in relation to major habitat features.

vicinity of terraces and thickets and least in eroded areas. While animals were often unevenly distributed along the line in a particular season, the total catch over the period of years was remarkably uniform from station to station (except as influenced by obvious habitat features), indicating that a consistent pattern of aggregation or "clumping" of individuals did not persist from one year to the next.

Weights and biomass.—As shown in Table 2 the average weights of individuals varied due to differences in the age structure of the population as discussed below. In general, individual size tended to increase when numbers were low and to decrease when numbers were high. This was especially true when peak years are compared with the year following. Thus, the average weights increased from 57.7 gms. in the fall of 1948 to 76.4 gms. in fall of 1949, and from 50.4 gms. in 1952 to 63.2 gms. in 1953. When the population density is expressed in terms of total weight or biomass, as shown in column 5, Table 2, fluctuations from year to year were less marked than when numbers alone are considered.

Natality.—The relationship between weight and reproductive activity in all females trapped since 1948 is shown in Table 3. No females weighing less than 60 gms. were found with embryos, nor were placental scars or other evidence of breeding discovered. This was also true of all other specimens taken in the region for which we have records. Meyer and Meyer (1944) found that in captivity *Sigmodon* began breeding between 40 and 50 days of age when females weighed 62–87 grams. As shown in Table 3 the per cent pregnancy and the average number

TABLE 2.—*Numbers, biomass and age distribution in population samples of Sigmodon, 1948–1954*

	Number		Total	Average wt., gms.	Estimated population biomass, kgms. per acre	Per cent adult
	♂	♀				
1948: Spring	3	3	6	36.9	0.22	17
Fall	28	31	59	57.7	3.40	16
1949: Spring	4	4	8	66.8	0.53	50
Fall	10	19	29	76.4	2.21	60
1950: Spring	0	0	0	—	—	—
Fall	8	9	17	42.0	0.71	19
1951: Spring	0	0	0	—	—	—
Fall	2	6	8	64.3	0.51	50
1952: Spring	0	0	0	—	—	—
Fall	33	18	51	50.4	2.57	24
1953: Spring	3	5	8	36.1	0.29	25
Fall	24	20	44	63.2	2.72	30
1954: Spring	0	2	2	103.9	0.21	—
Fall	1	1	2	79.5	0.16	—
Totals	116	118	234	—	—	—

of embryos in our field populations were much less in females between 60 and 80 gms. than in larger animals. We may conclude that females in the field, as well as in the laboratory, may breed when about 60 gms. in weight but are not fully mature until they reach about 80 gms. in body weight. No examinations of testes were made but since Meyer and Meyer (1944) found that males begin breeding at the same age as females, but at a slightly larger body weight, it is likely that few males in the field would begin breeding before attaining about 65–70 gram size.

Breeding occurred during both the May and the November trapping periods,

TABLE 3.—*Frequency distribution of pregnant females by weight classes*

Weight, gms.	Number females	Number with embryos	Per cent pregnant	Average no. embryos
0–20	11	0	0	0
20–40	26	0	0	0
40–60	17	0	0	0
60–80	23	4	17	4.5
80–100	7	5	71	5.4*
100–120	15	10	67	4.9*
120–140	8	7	88	5.6*

* Average for females between 80 and 140 grams is 5.2.

TABLE 4.—*Comparison of natality in low and high population years*

	Mature females, number	Pregnant females		Embryos	
		Number	Per cent	Av. no.	Extremes
Four low years (1949–50–51–54)	24	10	42	4.1	(3–6)
Three high years (1948–52–53)	29	16	53	5.7*	(3–8)

* The difference, 1.6 ± 0.49, is significant at 1% level ($t = 3.26$).

but the pregnancy rate was less in the fall. This would indicate, as do other records, that breeding tapers off in November, and hence late November or early December would generally be the correct period to sample the seasonal high. Of seven mature females taken in spring, six were pregnant (86%); while of 46 mature females taken in fall, 20 were pregnant (43%).

The number of embryos varied from 3 to 8 with the average in 30 fully adult females (80 gms. or more) being 5.2. It is interesting to compare this with Meyer and Meyer's laboratory colony where 44 litters averaged 5.6 with extremes being 2–10. Svihla (1929) reported an average of 4.75 young per litter in a small sample of Louisiana cotton rats. More interesting than averages, however, is the comparison of litter size in low and high populations years as shown in Table 4. The number of embryos was greater in years of high population density. These averages are not unduly weighted by the four young females (Table 3), since two occurred in the "low" year series and two in the "high." The difference (1.6 ± 0.49) is significant at the 1 per cent level.

Age distribution.—Comparison of age distribution of populations during low and high density years is shown by means of age pyramids in Figure 4. As has already been indicated the pattern of age distribution is strikingly different with three-fourths of the individuals being non-breeding juveniles (less than 60 gms.) during high density years as compared with only 55 per cent during low years. During the live-trapping study in 1949 when cotton rats were marked in February, May and June, August, and November very few individuals survived from

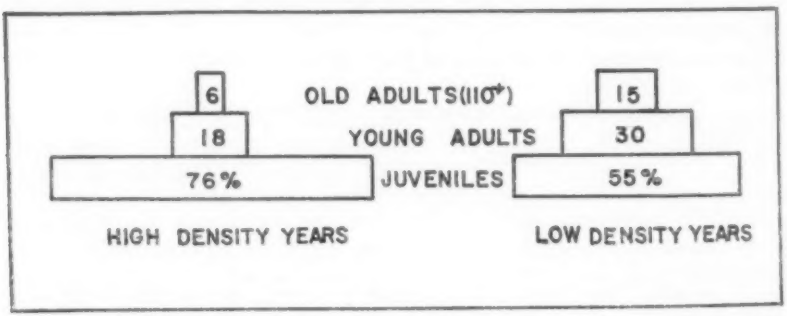

FIG. 4.—Age pyramids for high density years (1948–52–53) and low density years (1949–50–51–54). Juveniles (non-breeding) represent animals weighing between 10 and 60 gms., young adults, 60–110 gms., and old adults, 110 gms. and over.

one trapping period to another, and only one individual was recaptured in three successive periods. The record of this individual, a female, is suggestive of the growth rate in the wild. When captured on June 6 it weighed 15.0 gms. at 7 days of age; on August 21, 87.4 gms. at 76 days; and on November 12, 96.1 gms. at 159 days. Another female weighed 74.5 gms. on August 21 and 103.0 gms. on November 9, two and one-half months later. Since cotton rats weigh 6–8 gms. at birth (Meyer and Meyer, 1944) and increase in weight at the rate of a gram or better a day for the first few weeks, the 15 gm. female was probably about 7 days old. The smallest individuals caught on the trapline weighed between 10 and 12 gms. suggesting that young may leave the nest as early as the fourth day. The largest male was 280 mm. long and weighed 177.6 gms., while the largest female measured 274 mm. in total length and weighed 136 gms. (without embryos). Only a few individuals of either sex exceeded 125 gms. in weight.

To summarize, cotton rats in the field appear on the runways when a week or less old (weight 10–20 gms., total length 120–130 mm.), and begin to breed when two months or less in age (weight 60–80 gms., total length about 200 mm.). Females over 100 gms. and males over 110 gms. are probably five months or older. Since few individuals may be expected to live more than six months, the population turnover may often be complete every six months. With a species such as the cotton rat which begins to breed at an early age and rarely lives long enough to reach maximum size it is clear that average measurements of "adults" will vary according to the stage in the population oscillation (see also Komarek, 1937). Therefore, size should not be used as a criterion for the establishment of geographic races or subspecies unless the sample is very large and the stage in the population cycle from which it was taken is known.

SUMMARY

Autumn densities (Nov.) of *Sigmodon hispidus* (Figure 1) oscillated between 50 or more and 20 or less per double trapline during eleven consecutive years of sampling in an old field (Pl. I) that remained relatively stable in major habitat features. There were three well-marked "cycles" with major peaks in 1946, 1948, and 1952. Seven other species were taken but in small numbers (Table 1).

In six of the seven years in which spring (May) samples were also taken, the fall density was markedly greater than the spring density (Figure 2) suggesting a "northern type" seasonal cycle for *Sigmodon* in the Piedmont of Georgia as contrasted with a reversed seasonal rhythm (high in late winter and spring) that has been reported for *Peromyscus* in the Coastal Plain.

Except for the influence of obvious habitat features, such as old terraces, the total catch for the seven-year period was remarkably uniform from station to station in the 20-station lines indicating that there was no consistent pattern of aggregation that persisted from season to season and year to year (Figure 3).

In general, average age and weight of individuals tended to increase when the numbers were low and decrease when the numbers were high. Therefore, total biomass fluctuated from year to year to a lesser extent than total numbers (Table 2).

A small percentage of females between 60 and 80 gms. in weight contained embryos (average 4.5 per female); a much larger percentage of females over 80 gms. were pregnant with an average of 5.2 embryos (Table 3). The number of embryos was significantly greater in years of high population density (5.7) than in years of low density (4.1) (Table 4). A larger percentage of mature females were pregnant in the spring (May) than in late fall (November).

The age distribution in the population was quite different in low and high density years (Figure 4). In high years, 76 per cent of individuals were juvenile (10 to 60 gms.), 18 per cent young adults (60 to 110 gms.) and 6 per cent old adults (above 110 gms.). In low years the percentages were: 55 per cent, 30 per cent and 15 per cent.

On the basis of recapture data and Meyer and Meyer's (1944) study of captive animals it is estimated that cotton rats leave the nest at four to seven days of age (weight 10–20 gms.), begin to breed at two months or less (60–80 gms.), and reach 100 gms. (females) to 110 gms. (males) at five months of age. Very few individuals on a 1949 study plot survived longer than six months and few of the total catch (333 individuals) exceeded 130 gms. in weight, even though this is well below the maximum size recorded (177 gms.).

In a species such as *Sigmodon hispidus* that begins breeding at an early age and rarely lives long enough in the field to reach maximum size, it is clear that average weights and measurements of "adults" will vary according to the stage in population oscillation. Therefore, size should not be used in subspecific determination unless the sample is very large and the stage in the seasonal and annual population cycle known.

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ASPECTS OF A POPULATION STUDY OF CAVERN-DWELLING BATS

By John W. Twente, Jr.

In the course of a year's investigation (September, 1952, to August, 1953) of the habitat selection behavior of four species of cavern-dwelling bats, some data regarding aspects of the population dynamics of these bats were gathered. This paper is primarily concerned with *Myotis velifer incautus* (J. A. Allen), although *Corynorhinus rafinesquei pallescens* Miller, *Eptesicus fuscus pallidus* Young, and *Antrozous bunkeri* Hibbard are secondarily mentioned. The classification of Cockrum (1952) has been followed.

These bats were studied in gypsum caverns in south-central Kansas and northwestern Oklahoma (Fig. 1). These caverns vary from small tunnels to rather extensive underground passageways, and are quite variable in their climate and physiography. Those that are named are colloquially called "caves" although caves typically have but one entrance whereas caverns have two or more. In order to avoid confusion, these caverns have been designated by Roman numeral, but those with names that have been used in scientific literature of the region are listed as follows: Cavern II, Merrihew Cave; Cavern IX, Double Entrance "S" Cave (Hibbard, 1934), McMoran Cave of Cockrum (1952); Cavern XI, Natural Bridge; Cavern XII, Dancer's Cave (Hibbard, 1934); Cavern XIII, Triple Arch Cave (Hibbard, 1934); Cavern XIV, Havard Cave; and Locality XV, an unused mineshaft of a gypsum mine still in operation.

I would like to acknowledge the freedom allowed me by landowners of the region, without whose cooperation this problem could not have been completed. Particularly, I would like to thank Mr. and Mrs. John McMoran of Coldwater, Kansas, and Mr. and Mrs. Dewey Merrihew of Alva, Oklahoma. This paper is a part of a doctoral dissertation submitted to the graduate school of the University of Michigan. I would like to thank Professors Marston Bates, Dugald E. S. Brown, William H. Burt, Pierre Dansereau, Francis C. Evans, Claude W. Hibbard and other members of the faculty of the University of Michigan for their suggestions in the preparation of the thesis. Frederick E. Smith, of the University of Michigan, was of much help in the statistical interpretation of the data. Howard J. Stains, of the University of Kansas, made the identifications of the material found in the raccoon scats.

MOVEMENT AND HOMING

One method of checking movement of bats from cavern to cavern and from place to place within a single cavern is by banding. The data here gathered from banded bats indicate that movement from cavern to cavern occurs throughout the winter and that bats have no tendency to return to a particular place in a cavern during the hibernating season. If bats are taken several miles from the cavern of capture and released, the tendency to return to the original cavern indicates a tendency to home; scattering of bats to many caverns indicates that bats merely go to caverns that are available. The relation of homing to habitat selection is that the probability of a bat selecting a cavern suited to its metabolic demands is increased if it has a tendency to return to such a cavern after having been taken away from it. The number of caverns in the region studied that are not suitable for long periods of winter habitation are many (Twente, 1954*a*), and if the bat should choose one of

these, its behavior is to move to another cavern after having spent a short period of time in a torpid state.

Bats were banded on the forearm, using U. S. Fish and Wildlife Service Size "0" bird bands, from October, 1952, to early April, 1953, to test movement throughout the winter season and to trace movement from winter caverns to summer caverns. During this time, all *Corynorhinus*, *Eptesicus* and *Antrozous* that could be captured were banded. These included 155 *Corynorhinus*, 60 *Eptesicus*, and 8 *Antrozous*. Other *Antrozous* were observed, but they were inaccessible in a narrow crack in the ceiling of Cavern VIII. A hibernating population of around 5,000 *Myotis* in Cavern IX made gross banding impossible, and even if feasible, such banding would have caused disturbance which was not warranted in a habitat selection study. Consequently, a sample of 424 *Myotis* was banded in Cavern IX. *Myotis* numbering 487 individuals were banded from other caverns during the hibernating season.

Banding records show that *Myotis* move from other caverns, where they may be found in the fall, to Cavern IX, which is a wintering cavern for this bat. The usual behavior of *Myotis* after having been banded or disturbed in a cavern in the winter is to awaken, fly, and then become torpid again in the same cavern. Hibernating *Antrozous* banded from the crack in Cavern VIII and replaced in the same crack remained there after being handled. When *Corynorhinus* or *Eptesicus* were banded or disturbed, to read a band number, they invariably awakened and left the cavern and were not seen there for a period of a week to several months, if at all. The disappearance of bats from caverns after having been disturbed does not imply that such movement occurs in undisturbed populations. The reappearance of banded bats and the first appearance of unbanded bats (such as *Eptesicus* and *Corynorhinus*, of which all specimens seen were banded during the hibernating season), indicates that movement from cavern to cavern during even the coldest weather occurs in populations that have not been disturbed by banding studies.

Banding studies indicate that 151 (16.6 per cent) of the 911 *Myotis* banded were recaptured and that 33 (3.6 per cent) of those banded were in caverns other than the cavern of banding. Recaptures of the 155 banded *Corynorhinus* were 51 (30.3 per cent) although only three (less than 2.0 per cent) were found in caverns other than the cavern of banding. No *Eptesicus* were found in foreign caverns. These figures do not mean that *Corynorhinus* and *Eptesicus* tend to stay in the same cavern all winter, but rather that the bats were hanging in unknown caverns for periods of time before awakening and moving to other caverns that were being studied and where they were observed. The pattern of movement behavior of *Corynorhinus* and *Eptesicus* in the winter seems to be the selection of a cavern in which they may stay for a period of a few days to a month, depending on environmental conditions, and then after awakening from a period of torpidity, they fly out of the cavern and become torpid in another cavern. After awakening in this second cavern, they may return to the cavern in which they were first banded or move to another cavern. Of 49 male *Corynorhinus* banded in Cavern II during the hibernating season, 12 were recaptured there once after a period of absence from the cavern; six were recaptured twice; and three were recaptured three times. One male was captured on nine different occasions in Cavern II in the hibernating season. Of 48 female *Corynorhinus* banded in Cavern II, 13 were recaptured once and none were recaptured more than once. Of 13 females banded in Cavern VI, four were recaptured once; one was recaptured twice; and one was recaptured four times. One female was recaptured once in Cavern VI and once in Cavern II. The only male found in Cavern VI was recaptured there four times and once in Cavern II during the hibernating season. These data indicate either that the male *Corynorhinus* have a stronger tendency to return to one cavern than the females or that the males awaken and move more often than the females. The latter is probably the more accurate interpretation as Pearson, Koford, and Pearson (1952) stated that male *Corynorhinus* in California awoke more often than the females during the hibernating season. The same phenomenon was observed in this study until the middle of December, but from February on the behavior seemed to be the same. A differential behavior of the sexes from October to February, however, would account for the discrepancy in recaptures of males and females.

Banding returns show that, during the hibernating season, there is no tendency for *Myotis*, *Eptesicus*, or *Corynorhinus* to return to a certain place in a cavern. In Cavern II, where most of the *Corynorhinus* and *Eptesicus* were found during the hibernating season, unbanded *Corynorhinus* were present at nearly every visit to the cavern. This implies that the population is widely dispersed during the hibernating season.

Small numbers of *Myotis* may be found in Caverns I, II, VII and VIII in the winter, but winter concentrations of these bats are found only in Caverns IX, XIII, XIV, and XV. Over several hundred *Myotis* are constantly present during the hiberating season only in Cavern IX. A total of 88 Myotis banded in Cavern IX during the hibernating season were recaptured there. A female banded in Cavern IX in December was recaptured in Cavern XIV in February, and a male banded in Cavern XIV in December was recaptured in Cavern IX in February. This movement seems significant since it is a distance of 21 air miles. Whether or not this movement was caused by disturbance is not known. Griffin (1945) reported flights as long as 125 miles from one cave to another in the winter.

On March 26 and 27, 1948, Cockrum (1952) banded 1110 male and 890 female *Myotis* in Cavern IX. During this study 34 males and 46 females of those previously banded by Cockrum were recaptured at Cavern IX during the winter of 1952 and 1953. This represents 4.0 per cent of the original population. When these bats were recaptured, they were banded on the other forearm in order that they might be recognized at sight. It is reasonably certain that most of the remaining *Myotis* from this banded population Cavern IX were rebanded.

A constant 66.7 per cent yearly survival is the lowest survival rate in a population of animals having only one young per year that permits such a population to maintain itself at the same size. *Myotis velifer* is known to have but one young a year. A life table based on this theoretical, constant 66.7 per cent survival rate (Table 1) shows that 14.2 per cent of the population of 284 *Myotis* five years old and older bearing Cockrum's bands should still be alive during the fifth year after banding. Since only 4.0 per cent of the original population banded by Cockrum was taken throughout the winter, this would indicate that even though some were overlooked, a large number of bats should still be extant and living elsewhere.

Other authors have reported that bats tend to return to the cave of banding in succeeding

TABLE 1.—*Number of bats in year groups in a theoretical population of 1,000 with a constant survival rate of 66.7 per cent*

Year	Number of bats in each age group
1st	333
2nd	222
3rd	148
4th	99
5th	66
6th	44
7th	29
8th	19
9th	13
10th	9
11th	6
12th	4
13th	3
14th	2
15th	1
16th	1
17th	1
Total	1,000

years. Griffin (1940*a*) found only 1.7 foreign returns recorded out of every thousand bats banded in caves. Bels (1952) reported that about 90 per cent of the recoveries of 4,000 banded bats in Europe were made in the cave of banding. The information obtained from Cockrum's bands indicates that a much higher proportion of bats than found by Griffin or Bels do not return to the cave of banding after a period of at least five years.

Only twice during the winter, on December 11, 1952, and on March 16, 1953, was an effort made to read all of the bands on *Myotis* banded in this study in Cavern IX. This helps to account for the rather low percentage of returns (16.6 per cent); Griffin (1940*a*) pointed out that many banded bats are not captured at any one visit to a cave. Bands were read as they were discovered at other caverns throughout the winter. During the spring and summer, many bands were sighted on bats of all species, but very few were read since disturbance of individuals was avoided at these times.

The presence of a summer population of *Myotis* in Cavern VII which is much larger than the wintering population in the region studied indicates that large, wintering populations may be present in other caverns, probably to the south. A number of banded *Myotis* including many with double wing bands were sighted in Cavern VII in the summer indicating that at least some members of this population wintered in Cavern IX. A male *Myotis* was recovered in Alabaster Caverns near Freedom, Oklahoma, by Bryan P. Glass on February 24, 1954. This bat was banded on October 3, 1952, in Cavern II, which is about 25 air miles south-southwest of the point of capture. Cockrum (1952) reported the recovery of one of his bands 43 miles south-southwest of Cavern IX. These meager data indicate that there is at least some interchange of individuals from the various *Myotis* populations in the general area.

Three experiments were conducted to ascertain whether bats have a homing tendency. Fifty-two *Myotis* were taken from Cavern IX and released in an open wheat field (Locality V, Fig. 1) approximately seven air miles away in November, 1952. One of these bats was subsequently recaptured at Cavern IX. In December, 1952, twenty-eight *Myotis* were taken from Cavern XIV and released inside Cavern II, a distance of approximately 26 air miles.

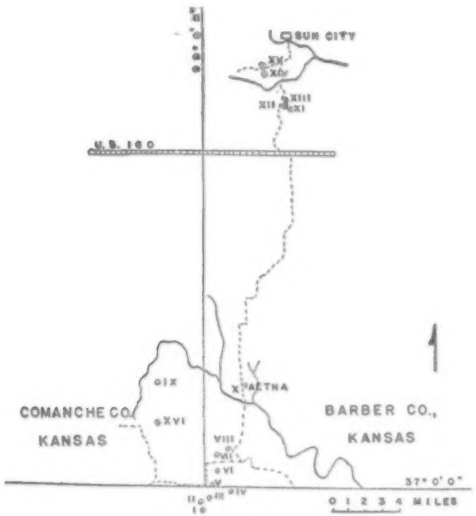

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FIG. 1.—The locations of the caverns where bats were studied.

Three of these bats were recaptured in Cavern XIV in February, 1953, and two were recaptured in Cavern IX in March, 1953. Of 27 *Myotis* taken from the gypsum mine (XV) and released at Locality V, one was recovered in Cavern II about two miles to the southwest and another was retaken at Cavern IX, seven miles north-northwest. The above homing data indicate that bats in the winter will sometimes return to the cavern from which they are taken, but that they will also fly to other caverns that are not in the direct line of flight from the point of release to the cavern of original capture.

A number of experiments were made in an effort to determine how bats find nearby cavern entrances. The procedure used was to collect hibernating bats from within a cavern on one day, place them in a cloth sack, and return to the same cavern on the next day. The bats were released in daylight, one at a time, usually within 50 feet of the cavern entrances. Cavern XIV was used primarily for these experiments as the entrances there were very small. The bats used were *Myotis* and *Corynorhinus*, whose behavior throughout these experiments was the same.

The first bat released in these experiments would fly around in circles as though lost, often returning to the bag in which there were squeaking bats of the same species. By squeezing these bags, it was found that audible squeaks could be stopped and the flying bats would not return to the bag when, to the observer, it was silent. They seemed to ignore the squeaks of the other species which were kept in separate bags. The second bat released would join, or be joined, by the first bat after an audible screech had been made by one of them. These would fly together, one bat a few feet behind the other, often alighting in trees for a few seconds. Subsequent releases showed the same behavior. Eventually, some of the flying bats would find the cavern entrance. After some of the bats had gone in, the other flying bats soon followed. The next bats released generally flew directly to the entrance. This indicates that sounds made by bats within may aid those flying outside to find the entrance, although to the observer no sounds could be heard coming from the cavern.

Another factor considered that may be of importance in the finding of cavern entrances by flying bats is vision. That vision is not an important factor in the daytime, at least, was substantiated by smearing heavy grease over the eyelids of bats before release; these bats behaved the same as normal individuals under similar circumstances. It is possible, however, that vision does play an important part at night when the bats' rod-vision eyes are not dazzled by daylight.

Smell was also considered as possibly aiding in the finding of cavern entrances. However, those bats whose nostrils were filled with a heavy, anaesthetic grease behaved as normal individuals, indicating that smell is probably not an important factor. How bats determine the general location of caverns after a long flight is not known.

SEX RATIOS AND AGE

The sex ratios of bats within the populations of different species were ascertained to see if there was differential mortality between the sexes or whether there were behavior differences between the sexes at the various seasons. A total of 74 male and 94 female *Corynorhinus* was examined in the course of the study. Nineteen male and 21 female *Antrozous*, and 28 male and 36 female *Eptesicus* were examined. Nursery colonies of over 100 adults were observed for *Corynorhinus* and *Antrozous*, however, and if these had been sampled the proportion of females to males would have been much higher. Practically all of the *Eptesicus* and *Corynorhinus* were examined while hibernating, as were 15 of the male *Antrozous*. Eighteen of the female and six of the male *Antrozous* were examined in the nursery colony. All of the above figures represent adult individuals. There were not enough data gathered for *Corynorhinus*, *Eptesicus*, and *Antrozous* to assess the possibility of differential mortality between the sexes.

On the basis of 1684 *Myotis* banded and examined from all localities, the sex ratio was 134.7 males:100 females (Fig. 2A). These figures are open to question since behavior of the sexes was somewhat different in the fall when much of the banding operation was carried out. Before movement to the wintering caverns, young males tended to gather in autumn pre-movement clusters in which might be included only one or two females. Such clusters,

usually numbering from 25 to 60 bats, were found in Cavern II on many occasions during October and early November. These autumn pre-movement clusters always formed at identical places in Cavern II. One of these places was a concavity in the smooth ceiling 15 feet above slowly running water. The other was six feet above dry guano within five feet of a clustering place of thousands of *Tadarida mexicana* (Saussure). These clusters appeared overnight, remained together for several days and stayed somewhat torpid depending on the surrounding temperature; at night they moved out of the cavern apparently to a hibernating colony. Within a day or two another cluster formed and the same process was repeated. Of 30 males banded from one cluster in Cavern II in October, three were found a week later in Cavern IX. Autumn pre-movement clusters of this kind have been examined at Caverns I, II, XI and XIV. Sampling such clusters, therefore, gives a preponderance of males which is not warranted for the sex ratio of the entire population, and illustrates differences in the behavior of the sexes.

Small clusters of *Myotis* near the entrances of Cavern IX during the early part of the hibernating season tended to be predominantly male as did all of the clusters at Cavern XIV. Small clusters were taken for sampling early in the study in order to get a relatively large number of bats with a minimum of disturbance to the other bats in the cavern.

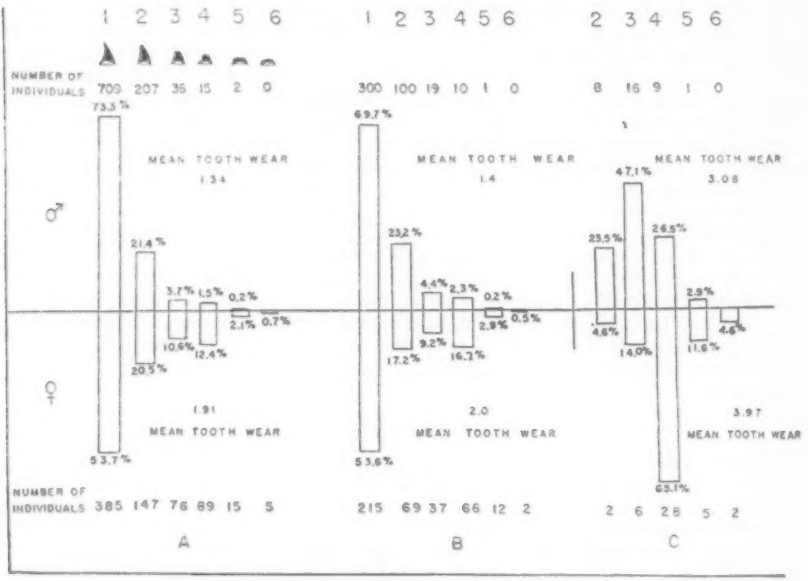

FIG. 2.—Age groups of *Myotis velifer* as determined by the amount of wear on the canine teeth. "A" includes the total number of *Myotis* sampled from all localities. 1684 individuals are represented, 57.4 per cent males and 42.6 per cent females. This includes those bats in "B", but not those in "C".

"B" includes two samples of *Myotis* from Cavern IX taken on December 11, 1952, and March 15, 1953. 831 individuals are included, 51.7 per cent males and 48.3 per cent females. None in "C" are included.

"C" represents the remaining members, in Cavern IX, of a population of 2,000 *Myotis velifer* banded in March, 1948. Eighty individuals were taken, 42.5 per cent males and 57.5 per cent females. (The histograms are based on 34 males and 43 females.)

At the gypsum mine (XV), on December 6, 1952, the ratio of male *Myotis* to females taken as singles was four to 18; this illustrates another behavior difference. Rysgaard (1942) found a ratio of 117 male *Eptesicus fuscus fuscus* (Beauvois) to 17 females in clusters and a ratio of 18 males to 48 females taken as singles.

In order to learn the actual sex ratio of *Myotis*, on December 11, 1952, and on March 16, 1953, an effort was made to collect what were considered to be relatively unbiased samples at Cavern IX. These samples are shown in Figure 2B, and represent 831 individuals with a sex ratio of 107 males:100 females. These figures were obtained by collecting one large cluster, several relatively small clusters, and many singles and doubles on each occasion. The large clusters, taken deep within the cavern, contained over 200 individuals each and had more females than males. The smaller clusters showed a preponderance of males. The sex ratio of those found in doubles was about equal and that of the singles showed slightly more females than males. The sum of these data indicates that the proportion of males to females in this population is about equal.

Other workers have indicated that differential mortality between the sexes occurs in bat populations although the sex ratio at birth is equal. Griffin (1940*b*) reported a sex ratio of 890 juvenile *Myotis lucifugus lucifugus* (LeConte) to be 450 males to 440 females (102.3 males:100 females). Cagle and Cockrum (1943) found the ratio of 432 juvenile *Myotis l. lucifugus* to be 219 males to 213 females (102.8 males:100 females). Hitchcock (1949) reported males predominant in five species of bats hibernating in Quebec and Ontario and on the basis of his data suggested that females may migrate elsewhere. Griffin (1940*b*) suggested that perhaps female cave bats have a greater mortality and in consequence a shorter life span. Eisentraut (1950) studied *Myotis myotis* in Germany and found that the survival of this species was an almost constant 60 per cent a year with the most losses the first year. These bats have two young a year. He reported that more young males than females survived until the next winter in their first year of life. In the course of an 11-year study, Eisentraut found that among the surviving bats of an original 1784, the males were more numerous than the females up until the seventh year at which time the sex ratio was about equal. On the eighth and ninth year the females predominated and on the tenth and eleventh the sex ratio was again equal. Mohr (1952) also found that females suffer a greater mortality than the males during the first year. The sex ratios for *Myotis* found in this study indicate that there is no differential mortality between the sexes.

The data from the *Myotis velifer* banded by Cockrum in 1948 and recovered in this study during the winter of 1952 and 1953 shows a ratio of 46 females of 34 males or 135.3 males:100 females. As the original population of 2,000 that he banded contained 55.0 per cent males (122.2 males:100 females), this figure is statistically significant (Chi square = 5.47, P. between .02 and .01 with 1 d. f.). However, as shown previously, since only 4.0 per cent of a theoretically 14.2 per cent surviving population was taken, it is possible that the actual sex ratio of the surviving bats is somewhat different. Mohr (1945) stated that there was no evidence of any significant sex difference in longevity or in the regularity of the return of bats to the hibernating quarters.

The sex ratio of the population can be better understood if the age distribution of the population is known. An arbitrary classification of tooth wear was established in an effort to relate wear to age and thus get an indication of the age structure of the population. Andersen (1917) estimated the ages of *Rhinolophus rouxi* from skulls on the basis of the wear of the first upper molar. He found that the canine was of little use as the effect of wear on this tooth is slower in the earlier than in the later years and the progress of wear was irregular. However, when studying live animals in the field, the canine tooth is the only one that can be observed without difficulty.

The maxillary canine teeth were observed to determine how much, if any, these teeth were worn. It was found that six groupings of tooth wear provided a usable system (Fig. 2A). Group 1 includes those bats in which the tip of the canine is unworn and pointed; Group 2, those in which the tip is slightly worn; Group 3, those which have a substantial portion of the canine worn away; Group 4, those in which the tooth is worn about half way

to the gums; Group 5, those in which the tooth projects only slightly above the gum level; and Group 6, those in which the tooth is worn completely to the gums. With the exception of *Corynorhinus*, which shows little canine wear, the other bats captured in this study were checked for the amount of canine tooth wear. Wherever doubt occurred, the bat was placed in the next highest wear class.

The population of *Myotis* banded by Cockrum five years previously provides an index for the relative value of such a tooth wear classification. Figure 2A represents the total number of *Myotis* examined throughout the study including those in Figure 2B. This sample represents *Myotis* taken in Cavern IX on December 11, 1952, and on March 15, 1953. Figure 2C includes those *Myotis* that Cockrum had banded in 1948. The youngest bats in the sample that Cockrum banded, then, were in their sixth year of life in the winter of 1952-53. Assuming that the population that he banded had the same proportion of bats in the various wear classes as shown in Figure 2B, it is possible to ascertain the relative value of the system used. Since no bats in Group 1 were found among the bats banded by Cockrum (Fig. 2C), it can be stated that Group 1 at its maximum limits can contain only bats four years old and younger. The small proportion of female bats in Group 2 indicates that it is unlikely that more than a small percentage of the total female population in this group is of this age. On the basis of a life table based on a constant survival rate of 66.7 per cent (Table 1), it is probable that the females in Groups 3 and 4 are five to seven years old, since 70 per cent of the original population would be in the first three years of life at the time of banding, and consequently would be the bats most likely to be alive after five years. The greater percentages of females in Group 4 than in Group 3 in both the total sample (A) and the old bats (Fig. 2C) would appear to be of significance since this humping of the curve does not occur in the male samples. Possibly, this greater amount of wear in the females throughout the samples is due to the greater metabolic demands on the female and the correspondingly heavier feeding while pregnant and while lactating. Mean tooth wear for the two sexes shown in Figure 2A, B, and C illustrate the above point.

The differential tooth wear of the males and females would seem to indicate that the mortality for the sexes is about the same throughout life, as would the sex ratio of the population shown in Figure 2B, which is not statistically significant. That actual age values could be assigned from this type of tooth wear study would appear to be doubtful.

Myotis caught in December, 1953, which had been banded the previous winter were usually assigned to the age group in which they had originally been placed, indicating that noticeable wear on the canines does not occur in one year. There were too few *Antrozous* and *Eptesicus* observed to be considered in a meaningful age-wear study.

Christian (1953) quantitatively studied the amount of wear on the maxillary canine teeth of 39 *Eptesicus f. fuscus* from Maryland. He constituted five groups of tooth wear, similar to the subjective groups utilized in this study and, correlating these data with annular growth rings on the teeth, concluded that *Eptesicus* in Maryland attained a probable mean maximum longevity of six years. Banfield (1948, 1950) reported banded *Eptesicus f. fuscus* from Quebec that survived more than eight years in two cases and more than nine years in one. Christian (1953) concluded that since the average number of frost-free days for Ottawa was 148 days and 180 days for Frederick, Maryland, the difference in the period of activity probably caused the longer life of the bats in the north. He suggested that these banding returns were perhaps exceptions.

The average number of frost-free days in south-central Kansas is 193, 13 more than in Maryland. The data in this paper indicate that Christian's conclusions do not apply to *Myotis*, and perhaps the matter should be more thoroughly investigated using banded bats of known age.

NUMBERS AND LIMITING FACTORS

It is difficult to understand the relative discrepancy in numbers of bats of different species in any given region. For example, two of the least common bats in the region studied (*Antrozous* and *Eptesicus*) have the highest reproductive potential, with two young per

year. On the other hand, two of the commonest bats (*Myotis* and *Tadarida*) have only one young per year. Estimates of the numbers of bats in the region studied were obtained by counting individuals and measuring the size of the clusters and calculating the number of individuals from the area occupied by the clusters (Twente, 1954*a*). The following estimates are for adult, summer populations: *Tadarida*, 25,000 to 50,000; *Myotis velifer*, 15,000 to 20,000; *Corynorhinus*, 300 to 500; *Antrozous*, 200 to 400. Summer estimates of the population size of *Eptesicus* were not attempted. Estimates were obtained by observation of nursery colonies. Where only females were present (*Corynorhinus* and to some extent *Antrozous*) these figures were doubled to account for males.

Twente (1954*a*) suggested that social behavior in bats does not tend to limit population size as it does in populations of certain other small mammals (Calhoun, 1952; Brown, 1953). This was explained on the basis that the problems of metabolic economy of bats do not allow for active behavior interaction between individuals. The social behavior of bats, apparently, is primarily limited to clustering, which is mutual and passive and which tends to maintain body temperatures suited to metabolic economy. This would benefit all of the members of the population, rather than just a few, as is the case where aggressive social behavior (dominance hierarchy and territoriality) is evident. Consequently, factors limiting population size of bats, other than behavior factors, must be sought elsewhere.

Pearson, Koford, and Pearson (1952) listed four factors that may limit the number of *Corynorhinus* in a particular region. These are: (1) disease, (2) the amount of food and water available, (3) the number and size of suitable roosting places in summer and winter, and (4) predation. They concluded that the population size is probably limited ". . . by the number of suitable roosting sites surrounded by an adequate food supply."

From the data gathered, there is little indication that disease is a limiting factor for any of the bats in the region studied. Nothing is known of the specific diseases of bats in this region. A very feeble male *Corynorhinus* was found at Cavern VIII on October 31, 1952. This bat was unable to fly although its rectal temperature was 34.4°C. This bat was fat and did not appear to be suffering from lack of food. It was banded and replaced where it was found. A week later this bat was found dead in the same place. Cockrum (1952) reported finding many dead *Myotis* hanging from the ceiling of Cavern IX in March, 1948. Only two dead *Myotis* were found in this cavern in the course of this study and these were found in April 1953. Eisentraut (1947) reported that most of the deaths of *Myotis myotis* occurred in the spring in females due to the rigors of pregnancy. An old female *Antrozous* was found dead in a crack in the barn at Aetna, Kansas (Locality X), on December 23, 1953. This bat apparently had not died while the summer population of *Antrozous* was inhabiting this barn, as no decay was evident. Two mummified *Antrozous* were found in the crack in Cavern VIII where these bats hibernate. Since few dead bats or bats that showed signs of disease were found, although they were constantly searched for, it would not seem probable that disease is an important limiting factor.

The climatic data, (Twente, 1954*a*), indicate that there are many places not occupied that are suitable for hibernation and for summer quarters for all species.

Nothing can be said regarding specific food items as they were not studied. However, it is unlikely that the amount of food would be a limiting factor for one species of insectivorous bat in a region that can support thousands of bats of another species.

Pearson, Koford, and Pearson (1952) discounted predation as being a possible factor in controlling the population density of *Corynorhinus* in California as no animals have been reported preying on this species. Allen (1939) stated that bats have few enemies. Data gathered in this study indicate that bats have many enemies. Hawks and owls apparently prey rather heavily on the bats in the region studied during the season when bats feed (Twente, 1954*a*). There is considerable evidence that raccoons prey on bats during the feeding and the hibernating season, but particularly the latter. In Cavern IX, it has been found that raccoons enter nightly and prey on bats that hang low enough to be reached. This was shown on four occasions when *Myotis* were bound with thread and wire and tied to the ceiling three feet from the floor of the cavern. These bats were invariably gone the following

morning and fresh raccoon tracks were present in the mud below the place that the bat had been tied. A single raccoon scat collected in Cavern IX in October, 1952, contained the remains of 14 *Myotis*, as indicated by the number of claws; this was probably the result of a single night's feeding. A raccoon scat collected from Cavern II consisted almost solely of *Tadarida* hair.

Probably one of the heaviest predators on bats in the region studied is the rat snake, *Elaphe guttata emoryi*. Hibbard (1934) reported finding one of these snakes on the floor of Cavern XII on September 3, 1933, that had recently swallowed a *Myotis velifer*. In the course of this study, these snakes were found in Caverns II, VII, VIII and XIV in both the winter and summer. These snakes hibernate in small cracks in the ceilings and walls of the cavern during the winter and are found in similar situations during the summer months. On July 13, 1953, in Cavern VII at 8:45 p.m., after the adult *Myotis* had left the cavern to feed, a medium-sized rat snake was seen on the ceiling. The posterior two-thirds of this snake was in a narrow crack and the anterior third was stretched toward a cluster of baby *Myotis*. A freshly-swallowed adult male *Myotis* was forcibly regurgitated by the snake at this time. Two other rat snakes had been marked by scale clipping in this cavern earlier in July so there were probably at least three snakes feeding on bats in this cavern. This snake, which can crawl along the rough ceilings of caverns, is a constant threat to sleeping young and adult bats alike. On December 23, 1953, the skin of a rat snake was found in the crack in Cavern VIII where a population of *Antrozous* spent at least two winters. Whether or not these bats move into their winter quarters while the snakes are still feeding is not known.

The sum of these data would seem to indicate that the population size of bats in this region may be controlled primarily by predators. As stated previously, in a population of bats in which the females each have only one young per year such as *Myotis velifer*, *Corynorhinus*, or *Tadarida*, a constant 66.7 per cent survival rate must operate if the population is to stay at the same size. This means that the yearly mortality cannot exceed 33.3 per cent. On the basis of a 30 per cent yearly mortality, this means that only about 1.1 per thousand of the population can be lost daily. A constant 50 per cent survival rate must operate if a population of animals in which the females have two young per year, such as *Antrozous* or *Eptesicus*, is to stay the same size. In these populations, only about 1.9 per thousand of the population can be lost daily if the 50 per cent yearly mortality rate is not to be exceeded.

Owl pellets have been found in which there were as many as six bats, and sparrow hawks have been seen to catch *Myotis* when the bats return to the caverns in the morning (Twente, 1954*b*). Predation by raccoons in the hibernating quarters would also account for many individuals. If the loss of babies that fall to the floor or whose mothers are lost is added, it would appear that few limiting factors other than predators would be necessary to account for most of the yearly mortality.

Predation is in one sense a density-independent limiting factor since predators apparently try to catch any bat that they chance upon. It would seem, however, that predation is also a density-dependent limiting factor since concentrations of flying bats seem to attract hawks and owls and allow them to catch the bats more easily than when the bats are flying singly. Concentrations of bats within caverns would seem to increase the likelihood of bats hanging low enough to be captured by raccoons or near enough to cracks to be captured by rat snakes.

The problem of the relative abundance of species in a given area remains unanswered at this time.

SUMMARY

This study of cavern-dwelling bats was made in gypsum caverns in south-central Kansas and northwestern Oklahoma from September, 1952, to August, 1953. Data on some aspects of the population dynamics of *Myotis velifer incautus*, *Corynorhinus rafinesquei pallescens*, *Antrozous bunkeri*, and *Eptesicus fuscus pallidus* are given.

Banding returns indicate that *Corynorhinus* and *Eptesicus* move from cavern to cavern throughout the winter and are not found in the same place in a cavern;

Myotis, when they awake from a period of torpidity, fly, and shortly thereafter become torpid at a different place in the same cavern. Some *Myotis* moved to other caverns, however, and several made winter flights as long as 21 miles.

Bats were taken from hibernating quarters and released at distances varying from seven to 26 miles away. The data show that they will sometimes return to the cavern from which they were taken, but that they will also fly to other caverns that are not in the direct line of flight from the point of release to the cavern of original capture.

Experimental evidence indicates that flying bats may find cavern entrances by following the sounds made by other active bats within the cavern.

Data gathered indicate that the sex ratio of *Myotis* is about equal although differential behavior of the sexes may lead to biased sampling techniques. More females than males of the other genera studied were captured, but this is not interpreted to indicate a differential mortality.

Arbitrary age groups of *Myotis* were established using the criterion of the amount of wear of the canine teeth. The data from these groupings indicate no difference in the longevity of the sexes, although the canine teeth of the females seem to wear faster than those of the males. Eighty *Myotis* of a population of 2,000 banded in March, 1948, by E. L. Cockrum, were recaptured in this study in the cavern of banding. The amount of wear on the canine teeth of these bats gives an index to the relative value of the system used, and the resulting conclusions are that definite year groups cannot be established. Since only 4.0 per cent of a theoretically 14.2 per cent surviving population of bats banded in 1948 was taken, it is suggested that the numbers of bats returning to the same cavern winter after winter is not as great as has been reported in the literature.

Since these bats have such a low reproductive potential, and since social behavior in bats does not seem to limit population size, it is suggested that predation on bats by hawks, owls, raccoons, snakes and other animals may be the primary factor controlling population density.

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HUNTING METHODS OF FISH-EATING BATS, PARTICULARLY *NOCTILIO LEPORINUS*

BY PRENTICE BLOEDEL

At least two and possibly five species in three families of bats have evolved the fish-eating habit. Two Asiatic species, *Myotis macrotarsus* and *M.* (*Rickettia*) *pilosa* are suspected of being fish-eaters simply because of their large feet and claws (Eisentraut, 1951; Allen, 1936). A third Asiatic bat, *Megaderma lyra*, has on two known occasions dropped remains of fish, together with frogs, mice and insects from night-roosting places, but its habits are unknown (Gudger, 1943). It may occupy an ecological niche similar to that of the large omnivorous *Phyllostomus* of the Neotropical region. The remaining two are New World species that are known to catch and eat fish and small aquatic crustaceans. First, *Myotis* (*Pizonyx*) *vivesi*, found only along the shores of Baja California and Sonora, apparently subsists almost completely on this diet; of many stomach dissections that have been made, only one has revealed insects, while all others have shown only fish and shrimps (Reeder and Norris, 1954; Burt, 1932). I have collected fecal pellets of *Pizonyx* from roosts on two islands just offshore from Guaymas, Sonora, and found it possible to separate them into two classes

according to whether they contain primarily decapod chitin or fish scales, the former pellets being dark red, the latter black. A sample that was thus sorted proved to contain almost equal volumes of each type of pellet. Since there were very few mixed pellets, one can infer that the diet of this species is about 50 per cent fish, 50 per cent shrimp. *Pizonyx* has been observed fishing, but the exact way in which it catches fish is still in doubt. My attempts to induce captive *Pizonyx* to catch fish in the manner described below for *Noctilio* have been unsuccessful. *Megaderma lyra* and *Myotis macrotarsus* have feet only slightly larger than those of their relatives, while *Pizonyx* and *Rickettia* have relatively enormous feet, with enlarged, laterally compressed claws, similar to those of *Noctilio leporinus*, the best known of the fishing bats and the main subject of this paper. In the absence of knowledge of the actual habits of any species, I would consider this anatomical modification of the hind feet the best possible evidence as to whether or not the bat is actually a true fish-eater.

The family Noctilionidae includes only *N. leporinus* and a few smaller species of the subgenus *Dirias*. *N. leporinus* ranges from the Caribbean and Mexico southward through the Amazon basin and the western lowlands of Colombia and Ecuador. In Panamá, where the observations to be reported were made, there are two species of *Noctilio*, *N. leporinus mexicanus*, the large fishing bat, and *N.* (*Dirias*) *labialis minor*; for convenience, I shall call these *Noctilio* and *Dirias*, respectively.

Noctilio has been suspected of catching and eating small aquatic animals since 1859, when Tomes quoted a Mr. Fraser as saying that the bats caught small shrimps while skimming over streams in Ecuador. The history of the ensuing controversy over whether or not they actually caught fish, and if so whether with the mouth, feet, or tail membrane, has been completely reviewed by Gudger (1945) and Eisentraut (1951). The results can be summarized thus: (1) either fish alone or insects alone or both have been found in the stomachs of these bats; (2) they have been seen skimming over and dipping into streams, lakes and ocean in such places as Trinidad, Panamá, Jamaica, Brazil and Venezuela, both in afternoon and at all times of night; (3) observers differed as to how the bats catch their prey, some giving credence to various forms of the notion that the interfemoral membrane is used as a sort of "impervious net" (a rather self-contradictory term), others believing that some combination of this membrane and the hind feet is employed. No one reached a definite conclusion, since the bats could never be observed really closely, and the latest opinions in print still differ (Gudger, Eisentraut, *op. cit.*). The latter, agreeing with the minority of earlier observers, has reasonably rejected the impervious net idea and accepted as most likely the method that is here shown to be actually used; *Noctilio* gaffs fish with claws of the hind feet, which are specialized for the purpose, and the interfemoral membrane is never used except occasionally as a pouch in which to confine the already captured fish momentarily.

The question of how fishing bats locate their underwater prey has also been answered heretofore only by speculation. It has been shown by Griffin (1953*a*, *b*) that insectivorous vespertilionids of northeastern United States can echolocate

small insects, and from many other observations and experiments it may be assumed that bats are generally able to detect echoes of their ultrasonic cries from rather small objects, at least as small as five mm. in diameter, and probably smaller. However, when high-frequency sound passes through an air-water interface, there is a great loss of sound energy, such that one could not certainly predict whether or not echoes from underwater objects would be sufficiently intense to be usefully audible to the bats, even at close ranges. Since *Noctilio* sometimes hunts successfully even in almost complete darkness, visual location of prey is unlikely. Some indirect evidence is here presented bearing on whether or not *Noctilio* can detect underwater fish, or simply fishes more or less at random.

MATERIALS, METHODS, AND ACKNOWLEDGEMENTS

While in the Panamá Canal Zone as assistant to Dr. Donald Griffin, who was gathering records of the high-frequency sounds emitted by various tropical bats, I became interested in the fishing activities of *Noctilio*; the work to be described resulted directly from Dr. Griffin's interest and encouragement, and Dr. H. C. Clark's generous offer of the use of the Gorgas Memorial Laboratory's Juan Mina field station, five miles northeast of Gamboa on the Chagres River. Part of my work was supported by a contract between the Office of Naval Research and Cornell University. To Dr. Harold Trapido, also of the Gorgas Laboratory, I am indebted for many helpful suggestions and information on the abundance of *Noctilio* and *Dirias* at Juan Mina. Dr. Trapido had previously established (MS) by observations and stomach analyses that *Noctilio* did catch fish in Panamá and that *Dirias* probably did not. Mr. Henry van Horn also supplied information on where bats could be found and helped in the collecting. Barbara Lawrence of the Museum of Comparative Zoology, Cambridge, generously permitted my dissection of some specimens of *Rickettia pilosa* and *Myotis macrotarsus* (stomachs empty). Lastly, I am grateful to Drs. O. P. Pearson and Seth Benson for critical reading of this manuscript.

At Juan Mina where I lived during April and parts of May and August, 1953, the Chagres is wide and slow-flowing; its surface is only rarely disturbed by mild breezes. The land around it is covered mainly by thick second-growth jungle, with a few small, man-made clearings. A colony of *Dirias* lived in the attic of Mr. van Horn's house, and both these and *Noctilio* could be seen in abundance flying over the river at night. During my stay there I observed both wild and captive *Noctilio* and *Dirias*, and photographed them in action in captivity in an attempt to prove, for each species, whether or not it caught fish, if so how, to what extent it lived on fish, and whether or not it was able to echolocate or otherwise detect animals beneath a water surface.

The captive bats were kept first in wire cages and later released on the screened porch of the laboratory building; this porch is about 40 x 8 ft., and 10 ft. high. For *Noctilio's* fishing activities, I provided a galvanized iron tray, 2½ x 6½ ft., 2½ in. deep, set in the center of the floor. The bats were captured over the river at night in a silk trammel net, about 8 x 25 ft., suspended horizontally just above the water. All animals that survived more than a few days of captivity subse-

TABLE 1.—*Species and relative abundance of fish taken by dip-net at night on the Chagres River*

Species	Body length	Abundance
	in.	
Astyanax ruberrimus Eigenmann	1–3	Abundant
Gambusia nicaraguensis Gunther	¼–1	Abundant
Allogambusia tridentiger (Garman)	½–2	Uncommon
Mollienisia sphenops gilli (Kner and Steindachner)	½–2	Abundant
Thyrinops chagresi (Meek and Hildebrand)	2–3	Common in certain shallow, clear-bottomed places, not found elsewhere
Cichlasoma maculicauda Regan	1–3	Uncommon (size given is for young only)
Philypnus dormitor Lacepede	2–6	Uncommon (size given is for young only)

quently recovered completely from the stress and minor injuries of entanglement in the net. Three *Noctilio* survived for over six months, and were eventually brought to the United States for further study.

Mr. William Follett of the California Academy of Sciences, San Francisco, has kindly identified a small collection of fish taken at night in a dip-net thrust among the grasses and floating vegetation extending from the shores of the river near Juan Mina. (Identifications also were checked by Dr. Carl L. Hubbs.) These fish represent the same species that I fed to captive bats, and are probably a fair sample of what the wild *Noctilio* were catching (Table 1). The two species listed as abundant are always found in numbers at night, "sleeping" just beneath the surface, and are most numerous in the places described below where *Noctilio* did most of its fishing.

HABITS AND FOOD OF DIRIAS

The smaller of the two Panamá species of *Noctilio* differs from *N. leporinus* only in the possession of a normal, unmodified hind foot, smaller size, and minor details of tooth structure; i.e., *Noctilio* differs from *Dirias* only in the specialized characters related to the fishing habit. However, since *Dirias* is the only close relative of the large fishing bat, and does a large amount of its flying over water, occasionally touching the surface, its diet is of some interest. In all, two series of stomachs have been examined by Trapido (*op. cit.*), and an additional series of ten by myself; none has contained anything but insect remains.

In August, 1953, to test the matter further, I confined seven adult *Dirias* on the porch, with two *Noctilio* that had learned to fish easily in the tray and were fishing every night during this experiment. In five days five of the *Dirias* starved to death rather than learn to catch fish in the tray, while the other two were recaptured on the fourth night and fed. These two subsequently survived in good health in a cage for a month on a diet of fish, which they learned to pick up from the floor just as described below for *Noctilio*. However, I think this indicates

nothing about *Dirias*' natural diet, for *Phyllostomus*, a large, partly carnivorous, partly frugivorous bat, and several temperate-zone insectivorous vespertilionids have also learned to eat fish in captivity. Therefore, one may conclude that *Dirias*, unlike its larger relative, is not a fishing bat. With the knowledge of *Dirias*' habit of flying low over water, of its ability to live on a fish diet, of *Noctilio's* method of capturing fish, described below, and with the assumption that the common ancestor of both species was probably a bat with structure, size and habits very much like those of *Dirias*, one can then imagine how the fishing habit and concurrent specialization of the hind foot evolved in *Noctilio*.

OBSERVATIONS AND EXPERIMENTS ON NOCTILIO

Wild *Noctilio* flying over the river were easily recognizable by their pale color, slow, steady flight, slow wing-beats, and large size. They were active all night, but seemed to do more fishing in the earlier part of the evening, before about 10 PM. Benedict (1926) saw apparently exceptional behavior of these bats off Monos Island, near Trinidad—in mid-afternoon they were flying over the ocean in company with pelicans; whether they were catching their own fish or feeding on the leavings of the birds, Benedict could not decide. Shallow lagoons and backwaters of the Chagres, where small fish were abundant, were favorite places for fishing; when the bats were flying over open water between these places they did no dipping. At night many of the fish rest in a relatively nonalert condition just beneath the surface, usually along floating blades of grass or among the weeds; it is unlikely that the majority of them would be alert enough to avoid the sweep of the bats' claws. When a bat was fishing, it coursed back and forth over a lagoon, either dipping in scattered places over the whole area, or less often repeatedly striking the same spot. Watching closely, I could see that the bats broke the surface with some part of the rear end of the body, but exactly how it was done I could not tell. Most observing was done with the aid of an eight-volt headlamp, some by moonlight, but one could hardly ever manage to be closer than about ten feet to a place that was struck by a bat. It was also impossible to tell from this distance whether or not a fish was caught on any particular dip, although one could occasionally hear the bat chewing as it flew close-by. (In the experiments with captives, it was always possible to tell by this sound if a fish had been captured.) The bats made dips varying from one to ten feet long, or occasionally a series of three or four short dips within fifteen feet. Their usual cruising speed was a little faster than that of our outboard-powered cayuca, which usually ran at about ten mph.; thus the bats' flying speed must have been about 18–25 ft. per second. I saw no indication that any bat actually pursued individual fish; rather they tended to fly smooth, undeviating courses, quite different from the usual sharply twisting erratic flight of small insect-chasing bats. Furthermore, several minnows confined for two nights to the upper two inches of water in a wood-and-cloth tray in a lagoon habitually visited by the bats failed to attract them as they flew by. However, I did see, on one or two occasions, a bat turn toward a surface disturbance made by one or more small fish. My impression was that the bats confined their fishing to

places that they had learned were usually crowded with fish, and that random dragging of the water in these places would yield sufficient food.

Since no roost of *Noctilio* could be found in the region, I set up a trammel net in places where I had seen the bats fishing. Often, watching this net, I saw a *Noctilio* approach it and then either turn away or stop, hover, and fly up and over it. Other species of bats also performed the same definite avoiding flight. Nevertheless, seven *Noctilio* were caught. The three that survived unhurt were kept for the first week in a wire cage, where they ate small fish placed alive on the floor of the cage. These they caught simply by crawling about on the floor until they blundered into a fish; they then seized them adroitly with the teeth, and climbed back up to the top of the cage to chew them. Both *Noctilio* and *Dirias* chewed their food twice—the first time quickly, depositing the large pieces in their large expansible cheek pouches (Pl. I, No. 1),— then chewing these pieces more finely before swallowing (*cf.* Gosse, 1847; Gudger, 1945).

On the ninth day of their captivity, I released two male *Noctilio* on the screened porch, and that night filled the tray with water and about 100–200 small fish. Having had their attention drawn to the water by my splashing, the bats tried and learned that night to fish successfully in the tray. On succeeding nights they were observed and photographed as they gradually became accustomed to light, noise, and my activity. Both still and motion pictures were made. The still pictures were made with flashbulbs at exposures of $\frac{1}{500}$ and $\frac{1}{1000}$ sec.

It is obvious from these pictures (Pl. I, Nos. 2–6), which are confirmed as typical by repeated observation and by about forty separate dips recorded on motion picture film, that the bats make no use of the interfemoral membrane during their fishing dips—the feet are held straight down, the membrane folded and tucked up between the legs (Pl. I, Nos. 3, 4). In a typical run, the bat tilts the body slightly more vertically as it approaches the water, then lowers the feet, raises the membrane and makes a dip from one to six feet long. The two males differed consistently in this, one always making shallow dips running the full length of the tray, while the other made plunges, which rarely extended more than two feet (contrast the wakes in Nos. 2 and 3). As the feet emerge at the end of a dip, the membrane is again immediately lowered and used for flight maneuvering, apparently its main function (Nos. 2, 5). However, if a fish is gaffed with the claws, the bat immediately brings the feet forward and seizes the fish with the teeth (No. 5). In this transfer, the membrane may or may not be used to confine the fish momentarily; in two sequences on the motion picture film, it was so used. If the fish is small, it may be devoured on the wing; otherwise the bat usually flies back to its roost and hangs up to chew its catch at leisure (No. 1). I have never seen the bats catch fish in any other way than gaffing with the claws. Further evidence on this point is the fact that if a bat drops a fish, examination of it always reveals small punctures, sometimes passing completely through the body. Also, on one occasion, when a bat caught a fish that was apparently too large to transfer to the mouth, it simply flew back and forth with the fish dangling from one foot until it dropped off. In one or two of the motion picture sequences, there are single frames suggesting that during a dip

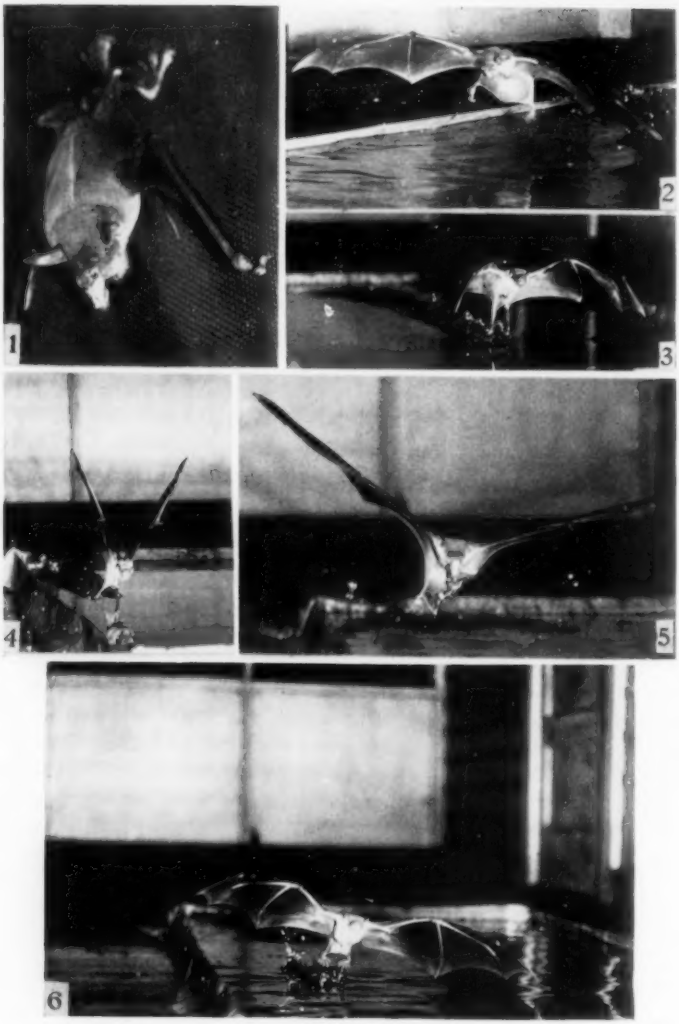

PLATE I

1. *Noctilio* hanging on screen, chewing freshly caught minnow. Hind foot 33 mm.

2. Rising from a dip, interfemoral membrane just being lowered. Splash just visible at right.

3–4. Typical long dips, with ripple trails visible. Note interfemoral membrane completely folded.

5. Bat just emerging from a short, successful dip, and in the act of transferring the fish from left foot to mouth.

6. Just emerging from short dip, showing spread claws.

a bat may sometimes quickly shoot a foot out to one side, presumably to catch a fish, but this may simply be an effect of unequal water pressure on an inadvertently twisted foot. However, if intentional on the bat's part, the action would imply close range echolocation of the fish.

In the light of these observations and photographs, I think it can no longer be doubted that *Noctilio*, and probably other fishing bats that have the same specialized hind foot, use the obvious method of gaffing fish. For this reason, and because of the mechanical difficulties of any method involving use of the tail membrane, I find it hard to believe Norris' observation (Reeder and Norris, 1954) that *Pizonyx* dragged the water with their tails, or that they catch fish and shrimp with the interfemoral membrane. My own experience suggests that no observation of this sort made at a distance of more than three or four feet can be relied upon to determine details involving distances of only one or two inches. What Norris probably saw was the bats dipping not their tails but their hind feet, and since the tails most likely were curved forward, although tucked up against the body, it would be difficult to determine the actual position of the tail when observing from above, as Norris was, on the stern of a ship.

The total consumption of the two bats was estimated to be about 30–40 fish each night per bat. The maximum actually counted was 38 for one bat watched until 4 AM. Since wild *Noctilio* are known to eat some insect food in addition to fish (Dr. Trapido has found both fish and insects in each of four *Noctilio* shot while flying over the Chagres), and since fish in the river are not usually quite as crowded as they were in the tray, these bats probably eat rather fewer fish in the wild. In the bats' favorite fishing lagoons, the density of fish near the surface was estimated to be about one-quarter of that in my tray when it contained the usual 100–200 fish.

Indirect evidence as to whether or not the bats can detect subsurface fish is provided by comparing their actual percentage of successful dips with the proportion to be expected if they were dragging the tray completely at random. The actual per cent of successful dips can be counted accurately, since, although it is impossible to see whether a bat catches a fish one can hear the chewing noises when the bat is successful, even if it does not return to its roost to consume the fish. The expected success of random dipping can be calculated from the following formula:

$$C = \frac{n\,Avf}{Al} = \frac{\pi a(b/\sqrt{2}+4)}{1080}$$

where C is the chance of at least one claw striking a fish of height and length a and b cm., respectively, with n fish in the part of the tray accessible to the flying bat. Estimated average values for a and b are 1 cm. and 2½ cm., while n is arbitrarily taken to be 10 per cent of the total number of fish in the tray, since most fish tended to congregate at the sides and ends of the tray, where the bat could not dip easily. Avf is the effective vulnerable area presented by the average fish turned at any angle to the bat's line of flight, the average angle being 45 degrees. Avf approximates an ellipse, whose long axis is the length of

the average fish divided by $\sqrt{2}$ and increased by 4 cm., the approximate length of the line of claws presented by the bat (No. 6). *At* is the area of a vertical rectangle perpendicular to the tray, bounded by the surface of the water, lines 5 cm. from the tray sides, and the bottom. For convenience, all n fish are considered to be in the plane of this rectangle, which involves the assumption that at any moment the images of all the fish could be projected on this plane without overlapping. Using this formula, the calculated proportion of successful dips can be compared with the actual success of the bats, for high and low densities of fish. If there are 10–25 fish in the tray (n = 1–2.5), the calculated success is .03 to .04, while the observed was, for one series of observations, .02. With 100–200 fish, calculated success is .13 to .26, and the observed, for 7 series, was .08 to .17. A series of observations was considered as a period in which a bat was feeding more or less continuously and caught at least ten fish. Although the method of calculating success involves some arbitrary estimates, and the agreement may seem in this case to be better than that expected from the error of the estimates, nevertheless I think this comparison shows that the bats do not catch more fish than would be expected on the assumption of random dipping. More definite evidence on this point is provided by the observation that the bats would attempt to fish continously for half an hour in the tray when no fish were present. Twice they even tried to dip into the dry tray. However, resting bats seemed to be aroused to fishing activity by splashing sounds. These facts show that although captive *Noctilio* were unable to detect the presence or absence of fish in the tray, they might in the wild be able at least to detect surface disturbances produced by groups of fish. However, Dr. Griffin has pointed out that it is also possible that the echo from the metal bottom of the tray might mask any echoes from fish that the bats might be able to hear under more natural conditions. Therefore I can conclude only that although I find no indication of echolocation of fish, it may yet be possible at close ranges. But accurate detection of fish is not necessary, since random dragging, with four times as much fishing as the bats did in captivity, would suffice to catch enough fish in the wild, judging by the amount consumed by captives and the density of fish in the lagoons.

SUMMARY

Although *Noctilio leporinus* has long been known to catch fish, its method of hunting has remained a matter for speculation. Photographic and observational evidence from these bats fishing in captivity is presented in this paper to show that *Noctilio* gaffs fish with the sharp claws of its extremely large and specialized hind feet. The question of whether or not *Noctilio* is able to detect under-water fish is discussed, and it is concluded that echolocation is possible and may conceivably be used at very short ranges, but that it is also possible for the bats to catch enough fish for their needs by dragging the water at random in places with dense fish populations, places that the bats are observed to frequent. The closely related *N.* (*Dirias*) *labialis* is not known to eat fish in the wild, and experiment showed that this species starves rather than learning to catch fish in

captivity under identical conditions to those under which *Noctilio leporinus* easily learned to fish. Other fish-eating bats with the same anatomical specializations as *Noctilio* probably employ similar hunting methods.

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THE FEEDING EFFICIENCY OF INSECTIVOROUS BATS

BY EDWIN GOULD

Griffin (1953) has recently suggested that insectivorous bats use their high frequency sounds not only for avoiding stationary obstacles but also for locating and capturing flying insects. Evaluation of this hypothesis requires accurate information about the sizes and sound reflecting properties of bats' insect prey, and this paper will assemble the pertinent data that I have been able to obtain both from previous papers and from the analysis of many digestive tracts of bats collected for this purpose. In addition to the types of insects captured the rate at which they are taken was measured whenever possible in order to judge whether a process of selective pursuit and capture is involved, or whether a random process akin to "filter feeding" could account for the efficiency actually attained. It would also be desirable to know the distances at which flying insects are detected; but to date no satisfactory methods have been developed for obtaining more than the rough estimate of this quantity included below for the red bat, *Lasiurus borealis*.

I wish to acknowledge my gratitude for advice received from the following entomologists, who identified many of the insect remains from bat stomachs; Asher Treat, John G. Franclemont, Howard Ensign Evans, W. T. M. Forbes, Clifford O. Berg, George Ball, Benjamin Henson, and Charles Wyttenbach.

Encouragement and helpful criticism were also provided by Donald R. Griffin. This work was supported financially by contracts between the Office of Naval Research and Cornell University (Zoology Department) and Harvard University (Biological Laboratories).

Data from previous work.—While many studies of bats' feeding habits have been reported, the results are often useless for the present purpose either because the insects could be identified only to order or family, leaving a considerable range of uncertainty as to their actual sizes, or because the identity of the bat itself was in doubt. The most extensive list of insects captured by known species of bats has been assembled by Poulton (1929) who includes many scattered observations reported by others. These records and most others do not give the insect sizes directly, but in such cases typical figures for the species in question have been obtained from Hampson's, CATALOGUE OF THE LEPIDOPTERA PHALAENAE IN THE BRITISH MUSEUM, or other standard entomological references.

The European long-eared bat (*Plecotus auritus*) provided most of the data summarized by Poulton; but this species can not be considered typical of the family Vespertilionidae, for it not only catches moths on the wing but also picks insects off the foliage of trees and bushes. Poulton (*loc. cit.*), Buckhurst (1930), Manwaring (1938), and Nicholson (1937) list 431 individual moths and butterflies of 22 species taken by *Plecotus*. The smallest of these was *Maniola tithonus* with a wingspread of about 30 mm., and the largest was *Vanessa atalanta* with a wingspread of 67 mm. The most common moths in these lists were *Mamestra brassicae*, *Caradrina cubicularis* and *Amphipyra tragopoginis*, with wingspreads of 46, 33, and 38 mm. respectively. Others of similar size were also numerous. The average wingspread of the moths taken by *Plecotus* can be estimated as about 45 mm. from the records presented by these four writers. Most of this data, however, was obtained from moth wings found beneath *Plecotus* roosts; many smaller insects may also be taken and these would not be represented in this compilation.

The noctule (*Nyctalus noctula*), one of the larger European bats, frequently takes beetles of approximately 20 mm. body length. Ryberg (1947) identified *Rhizotrogus solstitialis* and *Melolontha vulgaris* from this bat, while Poulton (*loc. cit.*) lists *M. vulgaris* and *Geotrupes stercorarius*. Eisentraut (1950) states that this species together with *Eptesicus serotinus*, *Myotis myotis* and *Rhinolophus ferrum-equinum* prefer relatively large insects. The closely related but smaller *Nyctalus leisleri* feeds at least to some extent, according to Poulton, on the dung fly, *Scatophaga stercoraria*, with a wingspread of 23 mm. The smaller European bats of the family Vespertilionidae are stated by Eisentraut to prefer Diptera and the smaller Lepidoptera.

The European horseshoe bats of the genus *Rhinolophus* belong to a different family from those mentioned above, and Moehres (1953) has recently shown that these bats use somewhat different types of high frequency sound for orientation, sounds characterized by higher and constant frequencies, longer pulse duration, and more directional emission. Poulton (*loc. cit.*) reports that the greater horseshoe bat (*R. ferrum-equinum*) was found to feed on at least two species of beetles, *Geotrupes spininger* and *Melolontha vulgaris*, 20 and 24 mm.

in body length respectively. Eisentraut (*loc. cit.*) states that the lesser horseshoe bat, *R. hipposideros*, like the smaller European Verspertilionidae, select Diptera and the smaller Lepidoptera.

Concerning American bats only a few records provide useful indications of the sizes of insects commonly taken on the wing. Huey (1925) found the remains of nine sphinx moths, averaging 77 mm. wingspread, beneath a roost of the California leaf-nosed bat, *Macrotus californicus* (Phyllostomidae). Poole (1932) mentions finding a small mosquito and a stink bug (*Nezara*, length probably about 16 mm.) in the stomach of a hoary bat, *Lasiurus cinereus* (Vespertilionidae). From the mouth of a Seminole bat (*Lasiurus seminolus*) shot while feeding, Harper (1927) recovered a green fly (*Chlorotabanus crepuscularis*, body length about 14 mm. (Stone, 1938). Orr (1954) lists several insects taken by *Antrozous pallidus*, but this species is known to catch Jerusalem crickets and probably other insects on the ground and it is not possible to determine which of the species listed by Orr were caught on the wing.

Insects taken from bats collected to study feeding efficiency.—During 1953 and 1954 many bats were collected by shooting, by means of trammel nets, or by collecting at roosts shortly after they had returned from feeding. In each case the weight of the bat and its stomach were recorded, together with the elapsed time since the first emergence of the species from its roost (usually observed on the same night, otherwise within a day or two). This time will be called for convenience the "feeding period," although it is of course a maximum time available for feeding, since at many roosts 20 to 30 minutes elapse between the appearance of the first and last bats. Also, the passage of food from stomach to the intestine has been neglected, so that the rates of food accumulation listed below are minima. The *Pipistrellus* and *Lasiurus* were not observed at their roosts, but their time of emergence is unlikely to have differed substantially from the other species. On several evenings insects were also trapped to aid in identifying the insect remains from the bat stomachs. Most of the bats were collected near Mashpee, Massachusetts, but some of the records were obtained near Concord, Provincetown, or Tyringham, Massachusetts; Ithaca, New York; and the Okefenokee Swamp, Georgia. Several bats were collected at the roosts before their evening flights commenced and all had completely empty stomachs.

Since bats are known to fill their stomachs under favorable conditions within a quarter to a half hour after their emergence from the roost (Poulton, 1929; Hamilton, 1930) particular attention was paid to the first few minutes of the feeding period. While the bulk of a bat's stomach contents consists of food too finely chewed for identification, the weight of stomach contents accumulated per unit time gives an indication of the bulk rate of insect capture, while the occasional identifiable fragment indicates at least some of the types of insect taken. Since identification is more likely when the insect is large or has hard parts in its exoskeleton, a list of types identified gives a biased impression of the actual food since the small soft-bodied insects will be much less likely to be recognized. Despite these limitations the results of this collecting program indicate limits to the range of sizes and numbers of insects captured by the species of bats studied.

Myotis lucifugus, the common little brown bat, provided the bulk of the data;

out of 68 of these bats collected, 33 stomachs contained fragments that could be identified as belonging to the orders Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, and Diptera. The identified beetles (Elateridae) ranged from 5 to 8 mm. body length and 10 to 12 mm. wingspread. An ichneumonid, *Cremastus* sp., had a body length of 8 mm. and a wingspread of 11 mm. Among the Chironomidae one *Chironomus* sp. was recovered with a 7 mm. wingspread and a body length of 8 mm. The smallest insect identified (*Metriocnemus mitis*, wingspread 3 mm., weight 0.2 mg.) was taken from the mouth of a *Myotis lucifugus* shot while feeding on the wing. Four of these bats were taken with reasonably full stomachs after 45 to 95 minutes feeding time, the stomach contents weighing 0.9 to 1.15 grams. Since the body weights of these four bats ranged from 5.5 to 8.2 grams, and since the maximum weight of stomach contents recorded from this species was 1.7 grams, their success at catching flying insects was impressive.

During August, 1953, bats were studied at Tyringham, Massachusetts, where they had become accustomed to hunt moths attracted by a light set up by Dr. Asher Treat; while not positively identified these were probably *Myotis lucifugus*, *Lasiurus borealis*, or both. On one occasion the wings of a moth of the family Pyralidae were dropped by a feeding bat; the wingspread of this moth was about 19 mm. and its body length about 10 mm. Another evening a noctuid moth, *Leucamia pseudargyria*, with a wingspread of 41 mm. was pursued by a bat up to a brightly lighted porch screen. Dr. Treat has since written that these bats "will and habitually do attack moths as large as *Crymodes devastator*" (body length about 30 mm., wingspread about 60 mm.).

On Sept. 2, 1953, a silver haired bat, *Lasionycteris noctivagans*, was shot while feeding over the sand dunes at Provincetown, Massachusetts, and from its mouth was recovered the remains of a stable fly, *Stomoxys calcitrans* (body length 7 mm., wing spread 14 mm.).

Twelve big brown bats (*Eptesicus fuscus*) were taken at Concord, Mass., from July 10 to August 7, 1954, after 25 to 112 minutes feeding time. Their weights ranged from 8.3 to 19 grams and all but one were young of the year. One had an empty stomach after 28 minutes, but another had captured 1.4 grams of insects after a feeding time of 33 minutes. The average rate of accumulation of insects, excluding the bat with an empty stomach, was 1.2 grams per hour; and the single adult *Eptesicus* had accumulated food at the average rate of 2.7 grams per hour. One banded big brown bat, released at dusk, was shot exactly 25 minutes later, during which time it had accumulated 0.5 grams of insects.

Most impressive of all were two *Pipistrellus subflavus* collected at Mashpee, Massachusetts, on August 4 and 5, 1953. These bats weighed 5.3 and 6.7 grams, and they had accumulated 1.4 grams and 1.7 grams respectively in 30 minutes of feeding time.

In late August, 1954, several red bats (*Lasiurus borealis*) were observed in the bright lights of a miniature golf course at Falmouth, Massachusetts, feeding actively on moths, beetles and other insects attracted to the lights. These bats did not appear in numbers at the lights until about an hour after dark; their first feeding period was evidently spent elsewhere. On some nights six to ten could be

seen at one time within a few feet of each other; sometimes two to four bats would apparently pursue the same insect. On three occasions bats flying relatively straight changed their course suddenly to dart towards and capture a moth estimated to be five or six feet to the right or left of the point where the bat began its sudden turn. Unsuccessful passes at flying moths were frequently observed; sometimes three or four successive attempts would be made. Once two bats made consecutive but unsuccessful attempts to catch a particular moth; only to have a third bat seize the prey. Twice it seemed clear that when one bat actively pursued a moth two others approached from several yards distance and joined in the chase. The high frequency sounds of these red bats followed a pattern generally similar to that described for feeding *Eptesicus* by Griffin (1953). This characteristic sound pattern of a feeding bat may have served to attract the others. The most abundant insect present was the adult of the army worm, *Pseudaletia unipuncta*; and the fact that the bats were feeding on this species was confirmed by a hind wing dropped by a bat while feeding. The average wingspread of several of these moths was 46 mm.

One 8.6 gram Seminole bat, *Lasiurus seminolus*, shot on the outskirts of the Okefenokee Swamp, Georgia on March 21, 1954, after 20 minutes of feeding time, had accumulated 0.5 grams of stomach contents.

The instances in which bats were clearly having a successful early feeding period are summarized in Table 1; and it is evident that rates of accumulation of one to two grams per hour are regularly attained by these bats under favorable conditions.

Discussion.—These rates of insect capture can be used to estimate the number of individual insects captured per unit time. Such estimates, however, require not only identification of an occasional fragment from the stomach contents but quantitative estimates of the proportion of the total catch that was contributed by insects of each size. Since only a very small fraction of the stomach contents escape reduction to an unidentifiable "soup," such assumptions cannot for the present be more than a rough approximation. For example *Myotis lucifugus* was shown to catch insects ranging in size from *Metriocnemus* with a weight of 0.2 mg. to moths weighing approximately 15 mg. The typical hourly catch of one gram for a successful *Myotis* might theoretically consist of 5000 *Metriocnemus* or 67 moths each weighing 15 mg., or any intermediate mixture. While neither of these two extremes is likely, it seems probable for *Myotis* that small insects weighing about one milligram predominate. Otherwise large chitinous pieces would have been found in the stomach contents.

If we assume, rather conservatively, that the one gram hourly catch consists on the average of insects weighing two milligrams, we arrive at an estimate of 500 individual insects captured per hour, or approximately one every seven seconds. Even the improbably high figure of 10 mg. for the average size of the insects captured leads to an estimate of 100 catches per hour, or one every 36 seconds.

Consideration should be given to the possibility that these bats feed by flying through dense swarms of small insects (such as chironomids) with their mouths

TABLE 1.—*Rates of insect capture attained by feeding bats. Only the more successful feeders are included*

Species of bat	Age	Body weight (grams)	Feeding period (minutes)	Weight of stomach contents (grams)	Theoretical rate of insect capture (grams/hour)
Myotis lucifugus	Adult	8	45	1.0	1.3
Myotis lucifugus	Adult	8.2	70	1.3	1.1
Myotis lucifugus	Adult	8.2	70	1.0	0.9
Myotis lucifugus	Adult	5.5	95	1.1	0.7
Average of 4 adult *Myotis lucifugus*		7.5	70	1.1	1.0
Eptesicus fuscus	Young	8.8	62	1.0	1.0
Eptesicus fuscus	Young	9.0	112	1.0	0.5
Eptesicus fuscus	Young	8.4	65	0.7	0.7
Eptesicus fuscus	Young	8.6	60	0.3	0.3
Eptesicus fuscus	Young	8.6	60	0.6	0.6
Eptesicus fuscus	Young	7.6	39	0.5	0.8
Eptesicus fuscus	Young	9.0	46	1.4	1.7
Eptesicus fuscus	Young	12.8	25	0.5	1.2
Eptesicus fuscus	Young	9.1	43	1.5	2.1
Eptesicus fuscus	Young	8.3	31	0.7	1.4
Average of 10 young *Eptesicus*		9.1	58	0.8	1.1
Eptesicus fuscus	Adult	18.9	90	4.0	2.7
Lasiurus seminolus	Adult	8.7	20	0.5	1.5
Pipistrellus subflavus	Adult	6.7	30	1.7	3.3
Pipistrellus subflavus	Adult	5.3	30	1.4	2.7

open, catching insects only by chance in a sort of filter feeding process. In *Myotis lucifugus*, however, the area of the open mouth is only about one square centimeter, and at a typical flight velocity of five meters per second the volume of air filtered would be about 1800 liters per hour. If the average weight of the insects were 2 mg., the average density would have to be 0.28 per liter (one in every 3.6 liters). Smaller insects such as *Metriocnemus* actually found in the mouth of a *Myotis* would have to occur at average densities of 2.8 per liter (one every 0.36 liters). Such densities are possible in swarms, but only during a small fraction of its feeding period could a bat possibly be flying through dense swarms even if these were selectively sought out. Even if one assumed that a bat flew through dense swarms as much as one tenth of the feeding period, the insect densities would have to be ten times the figures mentioned above in order to account for the actual rates of food accumulation on a random basis. Hence most of the prey must be secured by a selective pursuit of individual insects.

It is next necessary to inquire whether perceptible amounts of sound energy would be returned to a bat from such small insects as those captured by *Myotis*. To answer this question one would ideally wish to know: (1) the intensity of sound emitted by the bat, which can be taken as about 100 dynes/cm^2 (Griffin, 1950); (2) the distance from bat to insect; and (3) the proportion of the sound striking the insect which is reflected or scattered back towards the bat.

Over distances at which most insects are probably detected it is approximately true that the energy decreases as the square of the distance, both as the sound travels towards the insect and as the echo returns to the bat. Since energy is pro-

portional to the square of the sound pressure, the pressure of the returning echo should vary as the square of the distance from the bat to its insect target. On this basis one could theoretically calculate the sound pressures of the echo reaching a bat's ears; but a further complication arises because the smaller insects, at least, have dimensions comparable to the wavelength of the sound emitted by the bat. This results in an extremely complicated, sometimes periodic, relationship between target size and the proportion of the incident sound returning to the bat as an echo (Beranek, 1949, Fig. 313). Any detailed consideration of these matters is beyond the scope of this paper, but two important elementary points are consistent with the assumption that echoes from insects would be audible to the bats.

Even the smallest insects that are known to be captured (*Metriocnemus*) have wingspreads of about 3 mm. This dimension is approximately equal to the shortest wavelengths occuring at the beginning of the pulses that have been detected from this species on occasion. The typical initial frequency of *Myotis* pulses is about 80 kc., corresponding to a wavelength of 4.3 mm. But when a special effort was made to search for higher frequencies still earlier in the pulses (and lower in amplitude as picked up by the microphones) frequencies as high as 120 kc. were recorded (Griffin, 1950). The wavelength of 120 kc. sound is 2.9 mm. A very rapid decline in the energy scattered back to the bat will occur only when the target diameter falls well below one wavelength. Furthermore it is well known that these bats can easily detect wires as small as 0.5 mm. in diameter (Griffin and Galambos, 1941). Hence it is wholly reasonable to assume that echoes from 3 mm. insects would be detectable by *Myotis*, although more detailed analytical studies would be necessary to learn the effective range at which such small targets can be detected.

A second type of evidence that bats could actually hear echoes from insects has recently been obtained from preliminary experiments carried out with Dr. Griffin in which a bat was held in the hand and induced to emit pulses of high frequency sound directed toward an actual insect impaled on the end of a fine wire. Close beside the bat was placed the condenser microphone used to pick up the sound, but the microphone was also pointed towards the insect. Oscillographic records of echoes from the pulses emitted by *Myotis lucifugus* could be obtained from moths such as cecropia (*Platysamia cecropia*) and the common io, (*Automeris io*) at a distance from the bat to microphone of 50 cm. Some echoes were detectable at 50 cm. from a fluttering moth of the army worm, *Pseudaletia unipuncta*, having a wingspread of 35 mm. With the apparatus used, the minimum detectable sound pressure is far above the threshold of hearing of bats, if we assume that at frequencies of about 50 kc. they have a threshold equal to that of the human ear at 1 to 3 kc. The echoes that the apparatus could detect at 50 cm. must therefore be audible to the bats at considerably greater distances; and smaller insects at 50 cm. or less must also reflect echoes audible to the bat.

SUMMARY

An analysis has been made of the insects captured by bats on the wing, based both on a survey of published records and a program of collecting bats to analyze

the contents of their digestive tracts. Special attention was paid to the sizes of the insects and to the rates at which insects are caught; and this data is discussed in relation to the hypothesis advanced by Griffin that insects are located and captured by means of the bats' high frequency sounds.

The insects actually identified ranged in size from a 0.2 milligram *Metriocnemus* found in the mouth of a *Myotis lucifugus* to sphinx moths averaging 77 mm. wingspread reported by Huey to be captured by the California leaf-nosed bat *Macrotus californicus*. Even with the single species *Myotis lucifugus* the size of insect prey ranges from *Metriocnemus* with a wingspread of 3 mm. to beetles of the family Elateridae with wingspreads of 10–12 mm.

The rate at which bats fill their stomachs after the beginning of their evening flight indicates an impressive efficiency in catching insects. One gram per hour is not an uncommon rate in *Myotis lucifugus*. Maximum rates recorded were 2.7 grams per hour for *Eptesicus fuscus* and 3.3 grams per hour for *Pipistrellus subflavus*.

Making conservative assumptions regarding the average size of the insects captured by such species as *Myotis lucifugus* it can be shown that a random process akin to filter feeding cannot possibly account for these rates of catching insects. It is therefore probable that individual insects are located, pursued, and captured at rates of the order of one every few seconds.

The sizes of the insects are in all cases nearly equal to, or greater than, one wavelength of the sounds emitted by bats that catch them. Oscillographic records of echoes of bat sounds from insects at 50 cm. have been obtained, and there is good reason to believe such echoes would be audible to the bats. The evidence discussed is therefore consistent with the hypothesis that flying insects are captured by echolocation.

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OBSERVATIONS ON THE CALIFORNIA MASTIFF BAT

BY PHILIP H. KRUTZSCH

The mastiff bat is one of the largest and most impressive Chiroptera inhabiting North America. *Eumops perotis californicus* occurs most abundantly in southern California but its range also includes southern Arizona, western Texas and northwestern Mexico. Much of our present knowledge of the life-history of this bat stems from work by H. W. Grinnell (1918), A. B. Howell (1920*a*, *b*), A. B. Howell and L. Little (1924), P. H. Krutzsch (1943, 1945), and W. W. Dalquest (1946). The present paper synthesizes the foregoing citations and adds additional data. Many of the observations presented here were made in San Diego County, California and were gathered intermittently through most of the years 1935 to 1943 and in the summer months (June to September) of 1946, 1948, 1949, 1951, and 1953.

I wish to acknowledge the assistance of Messrs. K. Dixon, C. Engler, J. R. Homesley, R. Neil, and A. C. Olson, Jr., all of whom accompanied me at one time or another in search of these bats. Thanks are also due Drs. S. B. Benson and Hildegard Howard for permission to examine material in their care.

Eumops perotis californicus is a species of the Lower and Upper Sonoran life zones and has been found in cultivated areas, in rocky places where chaparral and live oak intermingle, and in more arid, rocky situations where vegetation is sparse. Mastiff bats utilize a variety of roosting places: von Blocker (1932) re-

cords one which was found hanging in a black acacia tree; Stephens (1906) lists a signboard and a tunnel as roosting sites; Howell (1920*a*, *b*) records several old buildings (either stone or wood) as roosts; Krutzsch (1943, 1945) and Dalquest (1946) report having found them in crevices in rocks; and we have one taken from under a window awning of an office building; and another from an inspection tunnel in a dam.

It seems likely that before the presence of man *Eumops* was chiefly a crevice dweller. Resting places in buildings are in cracks and narrow spaces. Perhaps rock crevices (where available) are preferred; in the San Diego area the only permanent colonies discovered were situated in such places. Other observers (verbal communication) record colonies in similar crevices near McKitrick (Iban McMilland) and near Bakersfield (Karl Koford), Kern County, California. The mastiff bat has been found roosting singly, but normally it is colonial. Colonies are small. Howell (1920*a*) considered 20 individuals a large number although he found as many as 70 bats in a single diurnal roost. A colony 1½ miles north of Barrett Junction, San Diego County, California, varied in population from year to year; a high of 60 individuals was noted in July, 1937 and a low of five individuals in July, 1948. Permanent roosting places in which conditions allow a "take-off" drop of 20 to 25 feet seem to be preferred. Nevertheless, there are records of bats utilizing temporary retreats that are but a few feet from the ground. Howell (*op. cit.*) was firmly convinced of the necessity for a long drop in order to allow the bats to "take-off," and he searched for *Eumops* only where such conditions existed. Howell remarked that he had often dropped bats from as high as he could reach from a standing position on a chair and had caught bats dropped to him from 30 feet above; in each instance these individuals refused to flutter and only opened their wings to break their fall to the ground. He also noted that these reactions were similar in warm or in cold weather. Howell was further impressed with a series of observations in which bats were found dead, presumably because of their inability to take flight from low roosting places.

It is clear to me from my own observations and those of Little (1920) that although these bats do prefer space for launching themselves into flight, they are capable of taking wing from a short distance above or from the surface of the ground. Experiments of the following type indicate that a confining quarter (lack of room for turning in flight) possibly is more restrictive to successful flight than is a minimum launching height. An individual released on the top of a laboratory table, 2½ feet above the floor, was able to take flight. The bat assumed a spread wing position. Wings were held almost fully open, feet spread wide. It raised and lowered its body in a series of pumping movements, each a little stronger than the next. Finally, it jumped into the air. A few full beats of its wings carried it the length of the 30-foot room; unable to turn, it flew headlong into the wall and dropped to the floor. Other bats were released under similar conditions, but none attempted to fly. Other experiments to determine minimum launching height were attempted. Most of these were unsuccessful. One bat flew when dropped from six feet in the air. Another was thrown eight or ten feet into the air and flew; others released in a like manner did not. All captive

animals were newly taken and uninjured. None remained in the laboratory more than 48 hours, and all were thought normal in vigor. That there is a marked reluctance to attempt flight is obvious; the reason for this reluctance is not known but is presumed to be due to a need for adequate launching height and flight space.

Diurnal roosting places may be occupied temporarily and infrequently; others apparently are favored and are regularly inhabited. The temporarily occupied localities are not marked by accumulated droppings and urine, characters common to long and habitually used retreats. Most temporary hiding places are visited by single individuals and possibly these animals are strays from some nearby colony. A regularly occupied roost in a vertical crack in a granite cliff, 1½ miles north of Barrett Junction was located in 1935 and observations on its occupants provide most of the data in this account. The Barrett Junction region is in the western foothills of San Diego County and is Upper Sonoran in character. The steep hillsides are marked by numerous granite outcroppings and are vegetated chiefly with chaparral (*Ceanothus* and *Adenostoma*) and scattered live oak (*Quercus agrifolia*). The valley floor is narrow, and Cottonwood Creek, a small permanent stream, provides moisture for a linear forest of willow (*Salix*), sycamore (*Platanus*), live oak and cottonwoods (*Populus*). The colony site has been visited at intervals in each of the years 1935 to 1943 and again in 1946, 1948, 1949, 1951, and 1953. Most visits were made in the spring, summer and early fall. The bats roosted in each of three large cracks in a granite cliff. Roosting places selected in these cracks were never less than 15 feet above the ground. The crack in which the bats were originally located is a vertical break in the granite cliff approximately 18 inches wide at the bottom and narrowing at the top, 20 feet above, to a width of three inches. This crevice extends into the rock for a distance greater than ten feet. Two other fractures in the same cliff, separated from each other by 30 feet, were used as alternate roosting places. These fissures are at an angle of 45 degrees from the vertical. The larger is 20 feet long and six inches wide at its widest point and the smaller is 10 feet long and four inches wide at its widest point. Bats were taken at one time or another in all three cracks. No preference between vertical and horizontal openings was noted; all were used indiscriminately. Other shallow crevices in the same cliff were never occupied. These openings were thought unsuitable to mastiff bats because they extended only a foot or two inside the cliff. The crevices that were utilized were inhabited during the months of April through October, and populations were greatest in June, July, and August. The number of individuals in the main roost varied from day to day, and on occasion a crevice would be deserted by all except the young. In such a case the adult bats usually could be located in one or frequently both of the other crevices. In the season when young were still unable to fly the bats always returned within 24 hours to the crevice harboring the babies. After the young were independent of the adults the colony often shifted from one site on the cliff to another without apparent provocation. Such shifting to alternate roosts is a behavior common to many species of bats, and has been commented upon by several authors: Orr (1954) for *Antrozous*, Pearson, Koford

and Pearson (1952) for *Corynorhinus*, and Ryberg (1947) for various species of bats in northern Europe.

The bats usually hang head downward with the entire body in contact with the substrate. Howell (1920*a*) found that the bats hung in horizontal rows or singly in a crevice with the body vertical and braced against bent wings. We found them less symmetrically arranged but always flat against the face of the rock upon which they clung. Mastiff bats are capable crawlers and are able to move very rapidly. Seemingly they back up and go forward equally well. Wings are folded tightly against the body, and bats use their radii to pull themselves forward. The feet apparently are used as steering organs, particularly when the animals are backing up. In this respect the long hairs of the toes seem to be tactile and bats explore to the rear with their feet, touching here and there in search of a free pathway. Little (1920) described an individual that he watched, stating that the bat backed up a vertical wall pulling itself upward with each foot alternately. Howell (*loc. cit.*) comments that *Eumops* is very agile on the ground and noted that they fold the wing tips above the back and scutter across the floor in a gallop with an overhand action of their arms.

Several observations on the Barrett Junction colony, continuous from early morning until well after darkness, indicated that mastiff bats have a rhythm to their diurnal activity. This rhythm appears to be influenced, at least in part, by variation in weather conditions. Bats were inactive in the early morning hours; no squeaking or crawling was noted until the sun had warmed the rocks. Usually on clear days the bats became active sometime between 10:00 and 10:30 AM. On foggy or cloudy and cool days bats remained inactive until after noon. The awakening of a colony of mastiff bats was not unlike the arousing of a covey of quail. First, one bat would squeak, followed by others. This squeaking continued undiminished, and soon bats could be seen moving about. Activity was considerably lessened after 4:00 PM. The bats hang motionless, and the only sounds audible are low chirping calls. This period of quiescence was continued almost until, and in some instances after, sunset when the bats again became active. Bats emerged only after complete darkness. A sloping, overhanging slab of granite adjoining the peak of the vertical crevice was utilized as a "take-off" site for bats roosting in this crack. Bats crawled to the edge of this rock and launched themselves into flight. The take-off always appeared labored; bats dropped steeply, wings only half open. The air pressure against the ventral surface of the wing membranes appeared to aid the bats in fully spreading their wings. The distance dropped seemed to vary with individuals, but it was usually from 7 to 10 feet. In full flight the wing beats were strong and even. Bats roosting in the horizontal cracks dropped directly from the rock wall into the air. When the nightly exodus from the roost began, just prior to launching themselves into flight, the bats usually uttered a series of loud, shrill, chattering calls. After becoming airborne the bats would often continue this call. Bats left singly at intervals of several minutes. On one occasion the first bat left at 7:25 PM. Seven others followed at 14 minute intervals. At 9:00 PM all bats had departed.

Howell (1920*a*) found that bats left their roost at late dusk and that the evening

flight lasted for only three quarters of an hour. This he presumed was followed by another flight just prior to dawn. I have conversed with other observers that have netted these bats at desert water holes (Cockrum near Tuscon) or watched them emerge from their diurnal roosting places (Koford near Bakersfield) and each mentioned that the bats appeared only after darkness. Repeated observations of the evening exodus at the Barrett Junction roost indicated that the bats normally emerged only after complete darkness. Here we are in agreement with other workers. However, we disagree with Howell (*loc. cit.*) as concerns the brevity of the foraging time. On numerous occasions a vigil was kept from sundown and early darkness (with exodus seen and heard) until near midnight and on no occasion were bats recorded returning to the roost by midnight. Bats must return at a later hour, although unfortunately a watch was not continued until dawn to determine the actual end of the foraging flight. The fact that bats are characteristically inactive during the forenoon may indicate that they forage late, perhaps until just prior to dawn.

Eumops apparently feeds on insects. Droppings collected from beneath their roosting places contain chitinous insect parts; however, these are so finely masticated as to be unidentifiable.

Night resting is a habit common to many of the species of vespertilionid bats. Most molossids do not habitually, but on occasion may, retire to resting places other than their own diurnal roost in the course of their evening foraging. At Alahambra, Los Angeles County, California during December, 1889, E. C. Thurber (see Grinnell, 1918) collected a mastiff bat from its resting place on a ledge over a door. He collected two others in the same month; both were found in similar situations. All bats were captured about 8:00 or 9:00 PM; it is possible that they were using these open locations as temporary night resting sites.

Observations indicate that males and females of this species remain together throughout the year. Howell (1920*a*) always found males and females in the same diurnal roosting places even just prior to the birth of the young. Howell (*loc. cit.*) records adults of the two sexes together in winter and spring, and I have records of a similar nature for spring, summer, and early fall. Little is known of the early reproductive behavior of *Eumops perotis*, but data available suggest that sperm production and insemination take place only in the spring as is characteristic for *Tadarida cynocephala* (Sherman, 1937) and *Tadarida mexicana* (Hartman, 1933). Variation in the gross size of the testes of adult male bats argues in favor of such speculation. For example, testes of adult males examined in April were found to be enlarged and were thought to be capable of producing sperm whereas testes of adult males taken in late summer were small and presumed to be inactive. If increase in the gross size of the gland is a valid criterion for indicating function (histological examination was not made) and sperm are not stored in the epididymis (which is not distended as in the fall breeding species, i.e., *Corynorhinus*) then one can presume that males are capable of inseminating females only in the spring.

Eumops perotis californicus normally has a single young but may have two. There is evidence that the date of parturition varies considerably. For example,

Iban McMillan found females with hairless young, and pregnant females on the same date in the colony at the Twisselman Ranch near McKitrick. As regards the Barrett Junction colony the following observations are available. On July 18, 1937, young of several sizes were found in the colony. Variation in size of young was again recorded on July 29, 1938. On this date two immature males were collected: one was nearly hairless and tiny and the other was furred and two-thirds grown. Such variation in development of young presumably is due to variation in the date of copulation; however, if copulation occurs in the fall and delayed fertilization is true then the variation in the development of young in a single colony is probably the result of differences in time of ovulation.

Young are born in the majority of cases by early July. The following observations on bats taken from the Barrett Junction colony are of interest. A female collected on April 5, 1941, was kept in captivity for six days; it refused food and grew weak. On April 10 the bat gave birth prematurely to a 20 mm. (crown-rump length = C.R.L.) embryo. On the following day, when preparing the mother as a specimen, a 15 mm. (C.R.L.) embryo was removed from the left horn of the uterus; the right horn was enlarged and presumably had contained the previously aborted baby. Four females were collected on April 6, 1939; each contained a single 18 mm. (C.R.L.) embryo. Data in regard to number and size of young and date of parturition are available from other places in California. On June 14, 1945, Dalquest and Benson (field notes and specimen labels) collected a series of *Eumops* at Silver Creek, 7½ miles southeast of Panoche, San Benito County, California; most of these bats were pregnant females each with a single embryo. According to data on the specimen labels their embryos ranged in crown-rump length from 33 to 42 mm. Howell (1920*a*) collected 13 adult females near Covina, Los Angeles County, California on April 15; each bat contained a single 19 mm. (C.R.L.) embryo. Howell (*loc. cit.*) also records two pregnant females obtained at Azusa, Los Angeles County on May 31. One of these parturiated a large, dull black baby on June 30. The earliest date that young were found in the Barrett Junction colony was June 29, 1938; the smallest of these was about one-third grown. Five juveniles were found on July 18, 1939; four were large, almost capable of flight, while the fifth was very small, naked, and with eyes yet unopened. On July 19, 1936, a single, very small, nearly naked young was found at the foot of the vertical crack. On August 6, 1941, an adult male and an immature female capable of flight were collected. A recently lactating female with milk still in the mammae and a nearly adult-sized young were obtained on August 29, 1943. On June 16, Howell and Little (1924) located 25 young bats varying from individuals which they judged to be about one week old to those three weeks or more in age. These young were found in the attic of a three story house near Covina, Los Angeles County. These data indicate that the reproductive season probably extends from March until early July, a period of approximately 125 days.

Eptesicus fuscus, *Tadarida mexicana* (Howell, 1920*b*) and *Tadarida femorosacca* (Krutzsch, 1945) may be found in the same attic or crevice in the rock with *Eumops perotis* but they roost separately from one another. Dalquest (1946) reported four other species (*Myotis subulatus*, *Myotis thysanodes*,

Pipistrellus hesperus, and *Tadarida mexicana*) within 100 feet of the roosting site of a mastiff bat. At the Barrett Junction colony *Eumops* and *Eptesicus fuscus* and later *Eumops* and *Tadarida mexicana* were found utilizing separate roosting places in the larger of the two alternate crevices. The smaller bats were in the narrow, peripheral portion of the lower end of the crevice, and the *Eumops* occupied the wide central portion. Four additional species of bats (*Pipistrellus hesperus*, *Myotis subulatus*, *Myotis yumanensis*, and *Myotis californicus*) were taken from tiny crevices in this granite cliff. *Eumops perotis*, like other molossids, has an extremely strong and penetrating odor which might well serve in attracting bats of other species as well as those of their own kind to the vicinity of a roost.

Howell (1920*a*) makes note of a gland located on the ventral throat surface. He points out its prominence in males and further indicates that it is particularly noticeable when they are sexually most active; presumably this gland secretes a substance which serves in attracting females of the species. In a later paper Howell and Little (1924) report the presence of this gland on a small juvenile female, but remark on its absence in the case of an adult female. They concluded that the gland may have originally been present in both sexes, not merely a secondary sexual character of the male. I have found this gland present and externally visible in both sexes. On young bats, particularly those that are almost naked, it is conspicuous as a small swelling slightly cephalad to the sternum. On adult males the gland is enlarged and apparently functional during the months October through May. Its position is easily marked in the male bats by a thick, oily, greyish-white secretion which accumulates at the external opening. Although not as easily located in the adult female, it can be found.

Eumops perotis californicus is apparently resident in southwestern California. I have records of its occurrence in all months (except January and December) in San Diego County, and Howell (1920*a*), Howell and Little (1924), and Von Blocker (1932) have records from Los Angeles and San Bernardino counties that exclude only January, August, and September. The mastiff bat is apparently absent in winter from its summer roosting place, 1½ miles north of Barrett Junction. This is likewise true of a colony located by Iban McMillan in a rock crevice on the Carl Twisselman Ranch, near McKittrick, Kern County, California. Mr. McMillan told me that bats were present in the early summer but absent in October. Perhaps there is a winter scattering, probably due to the unprotected nature of the crevice, to places not normally inhabited in summer. Possibly such a winter dispersal accounts for the presence of two individuals, one taken by C. B. Perkins in San Diego on January 11 and the other, also in San Diego, on November 21 by M. Sheppard.

Howell (1920*a*) pointed out that these bats can become torpid for short periods during inclement weather and thus, by minimizing their need for food, escape starvation. On the other hand, Howell (*op. cit.*) indicates that mastiffs forage during winter when the weather is suitable. He found one in mid-February, when when there was a skim of ice every night, roosting in an old packing house near Covina, Los Angeles County for three days. Howell (*op. cit.*) also speaks of often seeing them vibrate their body while hanging up; this might possibly be a re-

action for increasing body temperature. Individuals that I placed in a refrigerator set at 50°F quickly became dormant and remained inactive until aroused upon their removal to higher temperatures 10 days later. The arousal of these refrigerated individuals included a period of rapid shivering, followed by movements of the extremities that gradually accelerated to normal activity.

Two specimens of mastiff bats obtained during the summer of 1946 were examined for ectoparasites. One individual harbored several of the polyctenids, *Hesperoctenes eumops*. These ectoparasites were found equally often on the membranes and furred parts.

I have no record of vertebrates preying on *Eumops*. It seems logical to assume because of its size, strength, and late hour of foraging that this species is relatively free from predation. Mummified bodies of *Eumops* were found in and below the crevices we observed and have been found in most roosts described by other workers (Howell, 1920*a*; Dalquest, 1946). Perhaps this is indicative of a peripheral population or as Howell (*loc. cit.*) puts it, "the genus is a tropical one, and our species seems rather hard put . . . to survive."

There are two normal pelage colors (gray and brownish-gray) which apparently are found equally often in either sex; however, there is more brown pigmentation in the older individuals. An adult male (No. 4538 Los Angeles Museum) taken on November 23, 1938, at Los Angeles, Los Angeles County, California is entirely black. This is the only melanistic individual I have examined.

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THE GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION OF COTTONTAIL RABBITS IN MASSACHUSETTS

By Francis H. Fay and Edwin H. Chandler

The Commonwealth of Massachusetts is an 8000 square-mile area of rolling hills in the transitional zone of southern New England with elevations ranging from sea level in the east to more than 2000 feet in the Berkshire Hills of the west. Because its glacial soils are relatively poor for agricultural purposes, more than two-thirds of the state is woodland in various stages of secondary succession. The early faunal studies of Bangs (1894) and Nelson (1909) indicated that the New England cottontail (*Sylvilagus transitionalis*) was the only lagomorph other than the snowshoe hare (*Lepus americanus*) that was indigenous to this area and the states immediately north and south of it. Within a few years, however, Goodwin (1935) extended the known range of the eastern cottontail (*S. floridanus mallurus*) from southeastern New York to northwestern Connecticut, and subsequent investigations (Hosley, 1942) revealed the widespread occurrence of *S. floridanus* throughout most of Connecticut. *S. f. mallurus* was reported from Nantucket Island in 1920 (Anon., 1920), while a preliminary survey in 1949–50 also disclosed an abundance of this subspecies in central and southeastern Massachusetts.

Because *floridanus* is of primary importance as a game species over much of the United States, there is a wealth of published material on its habitat requirements and environmental relationships. Conversely there is a dearth of information concerning *transitionalis*. In the eastern states where both species occur, the usual practice in management studies has been to lump them together as one homogeneous population, either because it is assumed that both have essentially the same ecology or because *transitionalis* is not sufficiently abundant or important to warrant separate treatment. As early as 1894, however, Bangs pointed out some apparent major differences between the habitats of these two species which could be of fundamental importance in a system of sound biological management.

GEOGRAPHICAL DISTRIBUTION

The heads of more than 900 rabbits were collected in a statewide series. The bulk of these specimens was obtained by mail from hunters who had been supplied with return-addressed, waterproof-paper containers designed for this purpose. Identification was based almost entirely on cranial characters, viz., *floridanus* has a small supraorbital process and a broad postorbital that fuses in part to the squamosal, while *transitionalis* has no supraorbital, and its slender postorbital tapers to a point that is free from the squamosal. In a few cases in which skulls were badly smashed, the pattern of the head pelage helped to confirm identification. In practice the pelage of all heads was examined for the presence or absence of certain characters, e.g., the black spot between *transitionalis*' ears was 100 per cent consistent, while the white spot on *floridanus*' forehead was present on less than 50 per cent of that species and in some instances was represented by only two or three white hairs (Fig. 1). Ear shape and pelagination

were quite characteristic as follows: *transitionalis*, heavily furred inside, anterior outer border black, posterior inner border ochraceous to buffy, shape appears short and rounded; *floridanus*, sparsely furred inside, anterior outer border brown, posterior inner border pale buffy to white, shape appears long and slightly pointed. The apparent difference in ear length is real but is not statistically significant. It is partly an illusion caused by the thick pelage and smaller average ear length-width ratio of *transitionalis* (*transitionalis*, 1.47 ± .06; *floridanus*, 1.54 ± .08).

It is well established that rabbits from other parts of the United States have been widely introduced into Massachusetts within the past thirty years (possibly *S. f. alacer*, *similis*, and *mearnsi*), though the majority of whole *floridanus* carcasses examined in this study resembled most closely the description of *S. f. mallurus* given by Nelson (1909). Variations in pelage and a wide range of ear

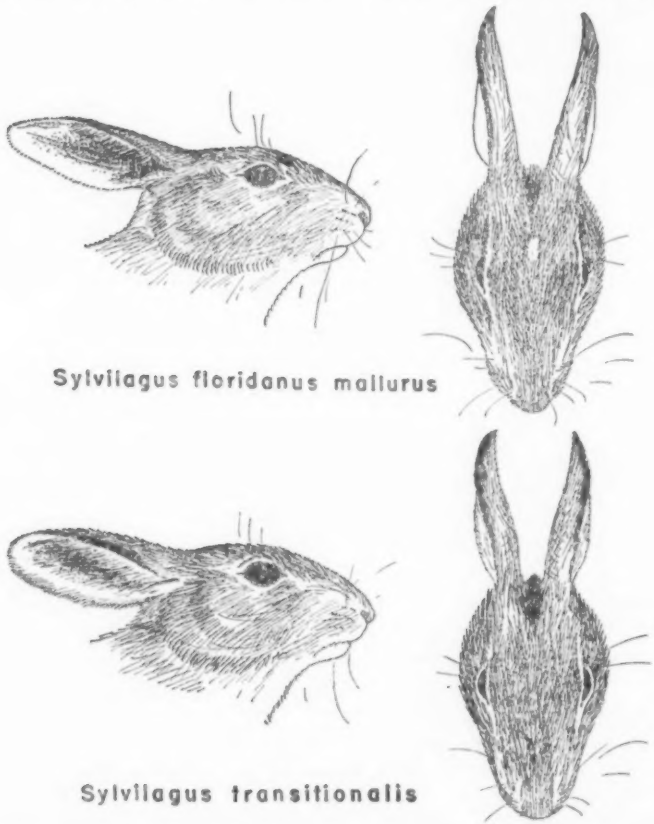

FIG. 1.—A comparison of ear shapes and head pelage of Massachusetts cottontails.

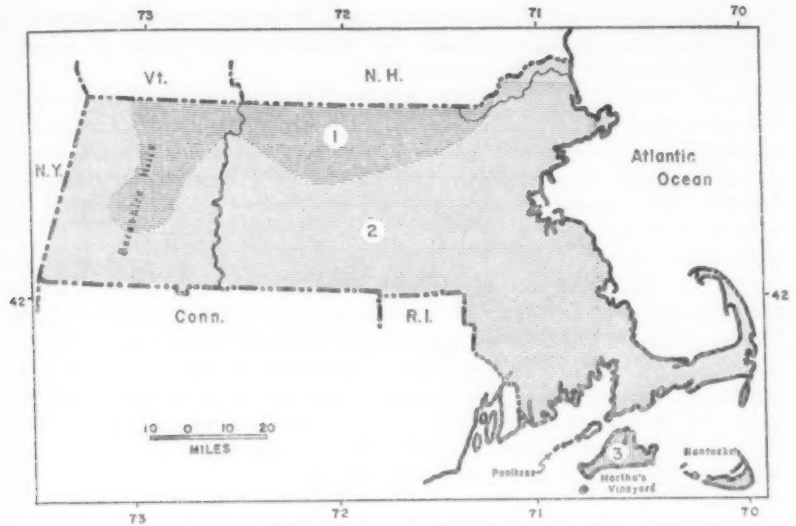

FIG. 2.—Distribution of *Sylvilagus* species in Massachusetts: 1. *S. transitionalis*, alone; 2. both species; 3. *S. floridanus* alone.

length measurements for *floridanus* (57.5 ± 4.0 mm.) as compared to *transitionalis* (56.0 ± 2.5 mm.) suggested that a mixture of subspecies or geographic races was present, but in most cases it was neither convenient nor possible to positively determine the subspecific identity. The map (Fig. 2) illustrates the widespread occurrence of *floridanus* as of 1952, with the only remaining pure cultures of *transitionalis* in the Berkshires and the north-central region. It is significant that the southeastern islands now support populations consisting entirely of introduced *floridanus* where *transitionalis* was once indigenous; while in the mainland area occupied jointly by both species the proportion of *floridanus* to *transitionalis* in our collection is more than 4 to 1. This northward expansion of *floridanus* appears to be a result of *S. f. mallurus* and introduced subspecies moving in from Connecticut, Rhode Island, and New York, coupled with direct introductions of midwestern rabbits and "farmed" stock within the state. The rabbit farm from which the latter were obtained was located on Penikese Island, where an intensively cultivated breeding stock of local and introduced rabbits supplied about 2000 cottontails of questionable lineage for release in mainland covers. The distribution of *floridanus* specimens suggests that this species may also be present in southern Vermont and New Hampshire, although small collections from these areas contained only *transitionalis*.

The collections of island forms of *floridanus* showed a surprising consistency of ear length measurements which differed from each other and from the highly variable mainland group as follows: Nantucket, 55.8 ± 2.5; Martha's Vineyard, 53.5 ± 1.3; Penikese, 51.1 ± 1.3. In general the crania of these insular races tend

to be incompletely formed, having a lacey pattern of ossification in the frontals, parietals, and squamosals. Whether this character is genetically or environmentally induced remains to be determined.

Smith (1950) has demonstrated that interbreeding readily occurs between some *floridanus* subspecies in captivity, and it might be expected under natural conditions as well. Dalke and Spinner also managed to induce *S. f. mallurus* and *S. transitionalis* to interbreed when confined together, though with some difficulty (Hosley, 1942). Earlier (Fay, 1951) some doubt was expressed regarding the occurrence of *floridanus-transitionalis* crossbreeding in nature, but additional observations have necessitated reconsideration of the evidence. In 1952 Mr. William A. Morris identified three young rabbits from the same nest as one *transitionalis* and two *floridanus* on the basis of skull and pelage characteristics, while in another litter four were obviously *floridanus* and a fifth had a very dark pelage closely resembling *transitionalis*. At least three specimens obtained in our collection had pelage and skull characters that were in questionable disagreement, the pelage resembling one species and the skull resembling the other. Bangs (1894) also mentions a few specimens that appeared to be hybrids. It is concluded, therefore, that crossbreeding does occur.

ECOLOGICAL DISTRIBUTION

In Massachusetts today there are many hunters who recognize the "conie" (*transitionalis*) and the "cottontail" (*floridanus*) as two different types of rabbits which generally occur in two different types of cover. Bangs (1894) observed these differences and stated that the eastern cottontail was found mainly in grassy areas and open southern woodlands, while the New England cottontail dwelt in thick brush, swamps, and denser woods. The possibilities of this statement in terms of management cannot be ignored in an area such as Massachusetts; therefore, in conjunction with our studies of geographical distribution an effort was made to determine the general nature of such ecological differences. The comparison has been made on the basis of forest types and the relationship of open land vs. woodland, open lands being defined as fields, gardens, lawns, and pastures.

The United States Forest Service (1949) divides the state into five major forest regions (Fig. 3). In actuality none of these divisions is homogeneous, none is entirely forested, and each grades imperceptibly into the next. There is, however, a basic similarity and continuity of forest classes within the prescribed areas, and, for the sake of general comparison, each type is considered below as a separate unit. Throughout most of these units there is rather extensive interspersion of woodland, brush, farm, urban, and water areas. Approximations of woodland and open land proportions have been adapted from the Census of Agriculture (U. S. D. A., 1952), Rozman (1940), and personal experience. The several small areas representing each forest type were all within the range of both cottontail species.

Shortleaf pine forest.—Cape Cod and the nearby islands are contained in this region, the characteristic forest type of which consists of open stands of pitch

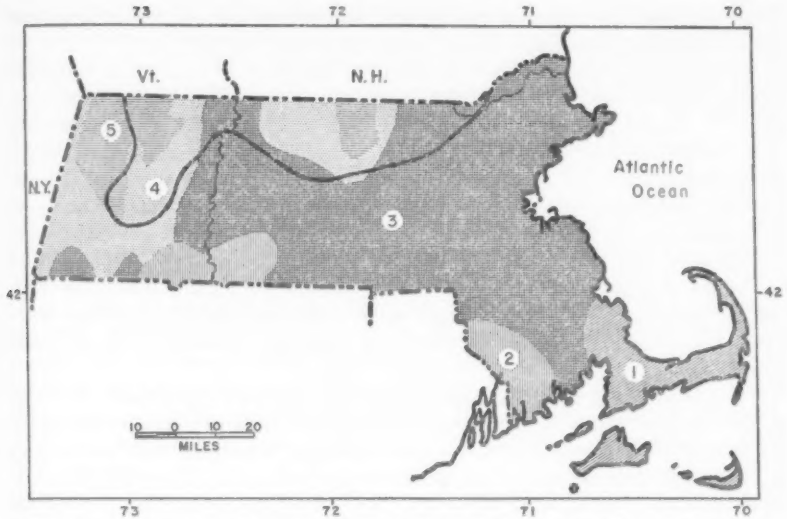

FIG. 3.—A comparison of forest types and cottontail distribution. Key to forest types: 1. Shortleaf Pine; 2. Oak-Hickory; 3. White-Red Pine; 4. Northern Hardwoods; 5. Spruce-Fir. Heavy black line marks the northern limit of *Sylvilagus floridanus*.

pine (*Pinus rigida*), white oak (*Quercus alba*), and scrub oak (*Q. ilicifolia*). In general the soils are rather sandy, supporting a typically sparse undergrowth of sedges, sweet fern (*Comptonia peregrina*), and blueberry (*Vaccinium* sp.). Where forest cover is absent the ground cover is often a dense tangle of wiry brush. Precipitation tends to be light and the temperature is moderated by the surrounding sea. About 80 per cent of the region is forest, swamp, and wasteland, practically all of which is potential cottontail cover. Excluding the island populations which, as mentioned above, are entirely *floridanus*, the proportion of *floridanus* to *transitionalis* in our collections from this region is 5:1. On a 100-acre tract, one third of which was open sedge meadow, 99 trap nights yielded six cottontails, all of which were *floridanus*.

Oak-hickory forest.—This is essentially the same open xeric woodland as the first, except that pitch pine is uncommon or absent. White and scrub oak and hickory (*Carya* sp.) constitute 50 per cent or more of the forest composition, singly or in combination. Most of Connecticut and southeastern New York are thus classified, with small tongues reaching into the Connecticut Valley and southeastern coastal plain of Massachusetts. About 75 per cent of this type is forest and wasteland, the remainder being farmland and urban areas. In the specimen collection from this region *floridanus* outnumbers *transitionalis* by nearly 8:1, though admittedly the sample is small. More than 40 *floridanus* and no *transitionalis* were observed alive and dead on a 320-acre tract of this type over a period of three years, while live-trapping on another small area (40 acres) yielded a fairly consistent 1:1 ratio during a four-year period. About 75 per cent

of the first area was crop and pastureland, and almost half the second was overgrown fields, the remainder of both being brush and woodland.

White pine-red pine forest.—More than half the state is included in this transitional forest which is principally characterized by the presence of eastern white pine (*P. strobus*) and/or red pine (*P. resinosa*) making up 50 per cent or more of the forest composition. The principal accompanying tree species are red maple (*Acer rubrum*), red oak (*Q. borealis*), and gray birch (*Betula papyrifera*). In general this is a comparatively more dense forest type than the first two and supports little ground vegetation other than hardwood sprouts and a sparse growth of blueberry and clubmosses (*Lycopodium* sp.). Approximately 70 per cent of the region is forest and wasteland. A small part of the northern sector in Massachusetts is occupied by *transitionalis* alone, while from the major portion where both species occur the number of *floridanus* specimens exceeded those of *transitionalis* by 4:1.

Three small areas were critically examined for species composition. The first, a 300-acre plot, including the urban center of Amherst and the campuses of the University of Massachusetts and Amherst College, was open land with a light interspersion of brush and small woodlots. Approximately 25 cottontails were observed there, and all were *floridanus*. The second, a fully forested area of 100 acres in the central Connecticut Valley, yielded only *transitionalis* when a live-trap survey was conducted. The third, a 90-acre tract in Upton, Worcester County, has been under close observation by the Unit and Division of Fisheries and Game since the spring of 1950. Initially, the entire area was composed of scrubby woodland and brushy overgrown pasture, but in the summer of 1950 a system of scattered clearings and small food patches was established, totaling about six acres. Prior to any land clearing the cottontail population was identified (by live-trapping) wholly as *transitionalis*, but a few *floridanus* were noted in the fall of 1950. The proportion of *floridanus* continued to increase in the live trap catch up to 1:1 in the spring of 1953, and it seems to be remaining about constant at that level (J. J. McDonough, personal communication, Massachusetts Division of Fisheries and Game).

Of ten *floridanus* specimens collected in the white pine region near the University of Massachusetts, nine were intimately associated with open land, and one was taken in a wooded area. Four *transitionalis* from the same region were all associated with woodland.

Northern hardwood forest.—Sugar maple (*A. saccharum*), yellow birch (*B. lutea*), beech (*Fagus grandifolia*), and basswood (*Tilia americana*) constitute 50 per cent or more of the total forest cover, singly or in combination, and eastern hemlock (*Tsuga canadensis*) is the principal conifer. Throughout much of the high ground of the Berkshires and the north-central part of the state this moist northern forest is predominant. Less than 70 per cent of it is woodland, most of the remainder being pasturage for dairy cattle. *Transitionalis* alone is present in nearly half of this region, while in the remainder the proportion of *floridanus* specimens was about 4:1. A 100-acre area of woods and brush in this type was surveyed by live-trapping, and the resulting catch was entirely *transitionalis*.

Spruce-fir forest.—The highest parts of the Berkshires and north-central sec-

tor are represented by this subalpine forest. Red, black, and white spruce (*Picea rubra, P. mariana,* and *P. glauca*) together with balsam fir (*Abies balsamea*) constitute the principal tree species. Generally the ground cover is composed of acidophils such as Labrador tea (*Ledum groenlandicum*) and sheep laurel (*Kalmia angustifolia*). About 70 per cent of the area is forested, and in the part occupied by both species of cottontail the proportion is 1:1 in our collection.

It is quite obvious that the above analysis is no more than a preliminary survey of a broad ecological problem. Nevertheless, the overall impressions gained are: (1) that in a heavily wooded region such as Massachusetts *floridanus* requires a certain amount of relatively open land in its environment, whereas *transitionalis* does not, and (2) whether a natural or human induced immigrant, *floridanus* has established a strong foothold in the state, possibly because of its better adaption than *transitionalis* to certain forest types and land use patterns. On the basis of our experience it seems reasonable to generalize further that *floridanus* is the better adapted to open lands in the shortleaf pine, oak-hickory, white pine, and northern hardwood regions and to the woodlands of the first two, while *transitionalis* is the better adapted to woodlands of the last two and the spruce-fir type.

In passing it is of interest that 89 per cent of 151 rabbits found dead on the highways were *floridanus*. Since even in wooded areas the roads are generally bordered by ten feet or more of weedy edge, this may be a reflection of *floridanus*' open land ecology. There are suggestions, however, that *transitionalis* tends to be more nocturnal than *floridanus* and might, therefore, be less vulnerable to highway traffic.

DISCUSSION

In recent years there have been a number of major changes in mammal distribution recorded in the literature, most of which seem to have resulted from human interference either through direct introductions or by environmental alteration. It is apparent that introductions have also played an important part in the spread of *Sylvilagus floridanus* into southern New England, though perhaps the principal factor involved has been the environment. Agricultural development in New England, which reached its peak about 1850 (Fowler, 1942), created an abundance of cultivated fields, and although some of these were abandoned prior to 1900, the further connection by road and rail undoubtedly provided adequate highways for the northward advance of *S.f. mallurus* whose open land needs were thus met. Furthermore, the broad avenue of the Connecticut River Valley which has been continually cultivated since early times appears to have been an excellent path for expansion. Once established in this new area, *floridanus* has replaced the native *transitionalis* over some of its former range. The mechanism by means of which this elimination has been accomplished (it is probably still going on) is not known, but two main possibilities exist, either one or a combination of which may be operative. The first and least likely is competition, involving food, cover, and space, and the second is reproductive parasitism. Since the general habitat peculiarities of the two species suggest slight qualitative differences in their food and cover requirements, it would be

expected that each species would inhibit its own potential increase more than that of the other, and both would therefore continue to exist together (Crombie, 1945). Although spatial competition may interfere with this, there is no observational evidence that it occurs under natural conditions. Hosley (1942) reported that "fighting was the chief cause of failure [of the two species] to breed" when held in captivity. However we cannot be sure that this was interspecific intolerance rather than mere sexual rejection or a result of artificial overcrowding, for Dice (1929) found fighting common even among captives of the same subspecies.

A pertinent example of reproductive parasitism among mammals is the elimination of *Lepus timidus* by *L. europaeus* from the open biotopes of southern Sweden and Scotland to which the latter is well adapted. Since the breeding season of *europaeus* is earlier than that of *timidus* males, some *timidus* females apparently bear sterile hybrids which eventually results in the complete exclusion of *timidus* from the mixed species environment (Udvardy, 1951). Indications that such a process may also be possible among Massachusetts cottontails have been found. In a preliminary survey, McDonough (personal communication) has observed that on the Upton study areas some *floridanus* females became pregnant in the spring a week or more before any *transitionalis* females. In addition it has been demonstrated that the two species will interbreed in captivity, and evidence has been presented in the foregoing of its occurrence in the wild. The scarcity of intergrades suggests that crossbreeding does not normally proceed beyond the F_1 generation which may mean that the hybrids are unable to perpetuate themselves because they are either sterile or "ecologically inviable" (Allee, *et al.*, 1949). The latter seems least probable.

An analysis of the specimens collected by hunters has led us to conclude that *floridanus* is unquestionably the most important of the two species from the standpoint of hunting and practical game management. Considering the entire hunter sample, the greatest number of rabbits collected per unit area was from the islands where the population is wholly *floridanus*. This was followed closely by the mixed species region from which more than three-fourths of the specimens were *floridanus*, while far below the others was the pure *transitionalis* region. Of the total *transitionalis* specimens the proportion from the "pure" area was significantly smaller than would be expected. This implies that rabbit hunting pressure is greatest within the range of *floridanus* and that most of it is directed at that species. It would therefore seem logical to aim most habitat management in Massachusetts towards *floridanus* production with lesser emphasis on *transitionalis*. Since Massachusetts is largely brush and woodland, it is expected that habitat management will depend heavily upon the skillful application of land clearing methods and patterns, as opposed to the usual midwestern practice of creating brushy areas.

SUMMARY

Massachusetts was formerly inhabited by one species of rabbit, the New England cottontail (*Sylvilagus transitionalis*), but since 1900 about three-fourths

of the state has been invaded by subspecies of *S. floridanus*. In an apparent response to changing agricultural practices in southern New England, the eastern cottontail (*S. f. mallurus*) has spread rapidly northeastward, supplemented by introductions of midwestern rabbits, and has completely replaced *transitionalis* in some local areas. Since a sample from the hunters' bag shows *floridanus* to be the more important game species of the two, it has been suggested that emphasis be placed on its management in the future.

Acknowledgements.—This is a contribution from the Massachusetts Cooperative Wildlife Research Unit, the U. S. Fish and Wildlife Service, Massachusetts Division of Fisheries and Game, the University of Massachusetts, and the Wildlife Management Institute cooperating. Part of the material was given by the senior author in a paper presented at the thirty-first annual meeting of the American Society of Mammalogists. The authors are particularly indebted to Dr. William G. Sheldon, Leader of the Unit, for his faithful guidance and criticism of this paper. We further extend our gratitude to Mr. James McDonough and Mr. Charles McLaughlin of the Massachusetts Division of Fisheries and Game, as well as to the many others, including rabbit hunters, whose patient assistance and cooperation helped make this study possible.

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OBSERVATIONS ON YOUNG BLACKFISH, *GLOBICEPHALA*

By Andrew Starrett and Priscilla Starrett

There is a paucity of information concerning the early life of whales, particularly of odontocetes. The recent paper by McBride and Kritzler (1951) on pregnancy, birth, and early development in captive bottlenose dolphins, *Tursiops truncatus*, at Marine Studios, Florida, gives the only detailed account of this part of the odontocete life. It is, therefore, thought that the following observations may be of some value and interest. They were made on Nantucket Island, Nantucket County, Massachusetts, during the spring of 1954. All comparisons with *Tursiops* made in this paper are based on the material presented in the reference already cited.

The first observations were made in the early afternoon of May 19, from the beach at the south end of Hummock Pond (the southwest ocean side of Nantucket), when a school of blackfish, *Globicephala*, came into view from the west. They were fairly close to shore and, through 7 x 35 binoculars, were easily identified by the characteristic black color, curved dorsal fin, and pot head. The school was moving very leisurely, individuals taking several seconds to roll from the time the head broke water until the animal disappeared. The school appeared rather drawn out, and continued to pass us for at least a quarter of an hour. After the first animals had reached a point to the southwest of us, approximately south of Surfside, they milled around until the entire school had reassembled, then headed southward out to sea. During the milling period, individuals could be seen moving in all directions until the school closed up. Although as many as twenty whales were visible at one time, a very conservative estimate put the size of the school at around forty to fifty. The length of time they were in sight, probably close to half an hour, made it possible to set up a spotting scope on a tripod for a closer look. Quite often an individual, when breaking water, would show the whole top of the snout, but only occasionally did the flukes come clear of the surface. Through the 35-power objective lens of the telescope it became apparent that there were young individuals in the school. They appeared to be from one-fourth to one-third the size of the adults and invariably one would be seen accompanying an adult, the two rolling almost together. The young blackfish had more sharply pointed dorsal fins and appeared to be lighter in color than the adults. The junior author, who had the best look at a young animal that came almost completely clear of the water, noted that it looked gray instead of black. That the young were probably suckling was indicated by the fact that occasionally an adult was seen to roll on its side, showing the characteristic long,

pointed flipper. This is the position assumed by the female *Tursiops* at Marineland during the first two weeks of suckling. On several such occasions, a young blackfish was seen to roll near the adult, presumably having nursed and now surfacing for a breath. It may well be that the slow speed at which the school was travelling was due to the presence of suckling young, since the young *Tursiops* observed by McBride and Kritzler nursed while the mothers were slowly "gliding," although they were otherwise able to keep pace with their mothers at top speed. Of additional interest is the fact that this school was seen during the day, since there is considerable evidence which indicates that blackfish are generally nocturnal (*fide* Kritzler, *op. cit.*: 321–334, 1952). The reasons for daytime activity in *Globicephala* are unknown, although it is possible that the presence of young animals in the school may have influenced their behavior.

Closer observations on a young blackfish were made possible when, on May 22, the authors found a female and newborn young of this species washed up on Eel Point, about 500 yards from the end on the Nantucket Sound side. The young was some thirty yards farther out on the point than the adult. That this particular young animal was undoubtedly the newborn calf of the adult was indicated by the extremely early age of the small blackfish and by the presence of what apparently was the placenta protruding from the still enlarged vaginal orifice of the adult (Pl. I). The proximity of the two animals is, of course, fairly strong argument in itself. The cause of death of the parent, as indicated by several large round holes in the body, was evidently machine gun fire from air force planes which are numerous in the area. Local fishermen indicated that it was not unusual for pilots to empty their guns at moving targets. The young animal undoubtedly died of starvation. The time of parturition relative to the time of death of the parent can only be assumed on the basis of comparison with data given for *Tursiops*. McBride and Kritzler noted that the placenta was passed as long as ten hours after parturition in one case. If comparison is at all valid, this would indicate some leeway in time for the blackfish. It was not mentioned, however, how long the vaginal orifice remained distended in *Tursiops*. On the other hand, the young *Tursiops* observed by McBride and Kritzler did not start to suckle for several hours, and the young blackfish we examined was fresh enough for it to be obvious from the digestive tract that little if any milk had been taken. The necessary part played by the mother in cetacean nursing would seem to indicate that the mother died before the young had time to nurse. The relative freshness of the baby whale points to the probability that it remained alive longer than the parent and very possibly followed the body until it beached. This would explain the proximity of the two when found, as it is more than likely that the school to which the adult belonged was somewhere in the Atlantic Ocean and not in Nantucket Sound when she was shot. The tides and strong winds often wash oceanic flotsam onto Sound beaches. In addition, Clinton Andrews, a Nantucket fisherman who has a comprehensive knowledge of the natural history of the area, has told us that even the smaller porpoises and dolphins are not often seen in the Sound area, preferring the deeper oceanic sides of the islands.

The newborn animal had apparently been beached shortly before we found it

PLATE I

Adult female blackfish with newborn young on Eel Point, Nantucket Island, Mass. Note placenta protruding from vaginal orifice of adult, and umbilical slit of calf. From a Kodachrome.

and was sunburned only on the exposed left side. The right side seemed to be in good condition as the skin was smooth and completely lacked any blistering. The color of the young whale, as seen on the good side, was ashy gray, with thin, wavy, subsurface black lines showing in various places on the body. No light ventral markings such as were seen on the adult were present. In agreement with the observations on newborn *Tursiops* at Marineland was the softness of the fins and flukes, the dorsal fin even flopping over to the right as did those of the *Tursiops*. Also, as in the bottlenose dolphins the tongue was fimbriated or ruffled around the edge and the teeth were not yet erupted, although their positions were plainly marked by bumps on the gumline. The teeth, when exposed by skeletonization, were conical with recurved tips, and were hollow for about three-fourths of their length. They ranged in height from nine to fourteen mm., and their bases, which were almost paper thin, ranged from four to eight mm. in diameter. It was not noted at the time whether the unpigmented flexure wrinkles described on young *Tursiops* were present, but an examination of kodachromes, taken when the blackfish were found, shows six more or less evenly spaced lighter gray lines on the animal's good side in much the same positions as those described for *Tursiops*. No obvious neck constriction was apparent. Unfortunately, we did not think to notice at the time whether any hairs were present and the photographs do not show enough detail to shed any light on this point. In contrast to the information recorded for *Tursiops*, the eyes of the newborn blackfish appeared to be still closed although the lids seemed completely formed.

Rough measurements were taken on both animals with the aid of a length of clothesline. The young whale was then partially skinned, the skull, hyoid apparatus, and entire left limb of the adult removed, and all parts staked out on the "moors" to skeletonize. Unfortunately, removal of the head of the adult lightened the corpse enough so that it washed away on the next tide, making further measurements impossible. The skeletal parts of both animals are now in the collection of the Mammal Division, Museum of Zoology, University of Michigan.

The measurements were all taken in direct lines without following the contours of the body or the curvature of the appendages. These measurements, in inches, for the adult and young, respectively, are as follows: total length from tip of upper jaw to center of rear margin of flukes, 174 and 69; from tip of upper jaw to insertion of dorsal fin, 54 and 25; length of left flipper from front of insertion to tip, 40 and 17; length of dorsal fin from front of insertion to tip, 33 and 14; width of left fluke from center of rear margin to tip, 17 and 9. Of interest is the size of the newborn young, roughly two-fifths of that of the adult. The high ratio is, of course, generally characteristic of cetaceans, where the young are necessarily precocious. In addition, it is interesting to note that the general body proportions of the newborn blackfish are essentially those of the adult. This too is most likely due to the need for immediate efficient swimming abilities. The young whale was surprisingly heavy, weighing at least two hundred pounds and requiring considerable concerted effort on our parts to drag it across the sand. Aside from what was concentrated on the snout, the blubber varied in thickness from about one-half inch on the sides of the caudal peduncle to a little more than an inch and a half in front of the dorsal fin.

The sex of the infant was not positively determined. Kritzler (*op. cit.*: 321–322) gives the external differences between the sexes of a number of blackfish stranded at St. Augustine, Florida. On our specimen, the external "inguinal morphology" was not decisive due to picking at the region by gulls, and internal evidence was not found because of the necessarily crude dissection. However, despite Kritzler's statement that "immature males resembled the females in body form," our infant whale showed quite distinctly two of Kritzler's characters for adult males: "the prominent hump extending from just behind the blowhole to the base of the dorsal fin" and "the pronounced crest on the dorsal edge of the caudal peduncle." These did not show on the mother.

DISCUSSION

Stranded schools of blackfish that have been recorded from Prince Edward Island in August (Needler, 1931) and the Gulf of St. Lawrence in September (Mathewson, 1935) have contained six-foot individuals. The two (out of 152) reported by Needler were apparently very recently born as indicated by the presence of part of the umbilical cord in each case. He suggests that they may have been born prematurely in the course of the stranding. He also reported one pregnant female in the school. The available evidence, then, shows that calving in *Globicephala*, in the region of New England and the Canadian Maritime Provinces at least, occurs mostly in spring with some calves being born in the fall.

There is no reason to doubt that calves are born all during the summer. If this is correct and if the blackfish gestation period is at all comparable with those estimated for the beluga, *Delphinapterus leucas*, (Vladykov, 1944) and *Tursiops* (McBride and Kritzler, *op. cit.*), then spring breeding is indicated for *Globicephala*. On the other hand, it is thought that the eastern Atlantic members of the genus mate during the winter months and there is considerable evidence that calving takes place for the most part in September (Fraser, in Norman and Fraser: 304, 1949). The presence of what appeared to be a rather uniform age class of young in the school we observed leads to the conclusion that much of the breeding probably occurs within a fairly short time within a school. A spring rut season has been described for the beluga (Vladykov: 111, 1944) and this may also occur in *Globicephala*.

Mathewson (*op. cit.*) and Needler (*op. cit.*) make no mention of any color difference in the young animals, although color changes in the skin due to exposure may have made differences less obvious. Needler did not see the whales himself until five days after they were stranded. The seven and one-half-foot male *Globicephala* kept at Marine Studios, the smallest of those found stranded by Kritzler (*op. cit.*), still had nursing tendencies and was apparently black. The logical inference here is that formation of the black pigment occurs rapidly after birth. Perhaps the black lines observed by us in the skin of the newborn blackfish were the beginnings of the pigmentation process. This is in contrast with the beluga which undergoes four color changes, associated with age, which are due to the *loss* of pigment from the epidermis. They go from dark brown at birth, to bluish, to grayish-white, in year classes until the fourth or fifth year when they attain their "typical" milk-white adult coloration (Vladykov, *op. cit.*: 65).

Due to the present confusion as to the status of the named species of *Globicephala* it was not felt that a definite specific name could be applied in the present case. Present on the good side of the adult's neck was a patch of gray, similar to the color of the young. This undoubtedly was part of the head of the kedge-shaped light marking present on the ventral surface of the body in some species. Since southeastern Massachusetts is within the supposed range of the common blackfish, *G. melaena*, our specimens were at first assumed to be of this species. However, the flipper-to-body-length ratio of about one to six in the adult female, if a valid character, would identify these specimens as *G. macrorhyncha*, generally thought of as a more southerly species. It is probably safe to assume the dead whales were of the same species, and very likely from the same school, as those observed alive.

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Museum of Zoology, University of Michigan, Ann Arbor, Received September 25, 1954.

MORE PIKED WHALES FROM SOUTHERN NORTH ATLANTIC

BY JOSEPH CURTIS MOORE AND RALPH S. PALMER

Several years ago the stranding of a rare species of whale on the Florida Keys stimulated one of us to attempt to discover just what ranges of marine mammals could be shown to extend into Florida waters. When the results of this investigation were recorded (Moore, 1953), one of the interesting items revealed was the occurrence of the little piked whale, *Balaenoptera acutorostrata*, in the Gulf of Mexico. This midget member of the finback family of the whalebone whales was known before this to occur only as far south as Long Beach (lat. 39°30′ N.), New Jersey, where one stranded in the fall of 1866 (Rhoads, 1903). Its previously known range on the eastern continental shelf of North America, Anderson (1946) has succinctly described as, "... rare in Baffin Bay, common on South Greenland coast and in Davis Strait, and on Labrador and Newfoundland coasts; [occurs in] Gulf of St. Lawrence, and south to New York and New Jersey." Jonsgaard's (1951) reference to a record from Cape Hatteras is a misinterpretation. This indicates that off the eastern North American coast it was known to be common between 70° and 50° north latitude and to occur south to about 40° until our above-mentioned report extended this south to just below 25°. This southernmost record of the species for the North Atlantic Ocean was based upon the February, 1949, stranding of an adult piked whale in the Florida Keys. A further extension of the animal's known range up into the Gulf of Mexico at 30° latitude was reported on the basis of an adult's skeleton from near Spring Creek, Florida.

On December 30, 1953, the authors heard that a large "blackfish" had stranded itself by the Seven Mile Bridge of the Overseas Highway about a half mile east of Little Duck Key (at lat. 24°41′ and long. 81°14′). With the encouragement and assistance of Daniel B. Beard, we visited the area at once and saw the whale from the bridge but did not reach it until the next day when John J. Brantner of Marathon took us to it in his boat *Fiesta*. The whale lay on its left side in three feet of water on a bar. Great portions of blubber and flesh had been bitten away, evidently by sharks. The tongue had been so removed from beneath the lower jaw. Parts of the viscera and much of the propulsive musculature were also gone. The right eye and the jaws were undamaged and revealed the animal to be a whalebone whale. The twin blow holes could be felt beneath the surface, but had also been excavated somewhat by the sharks. The right flipper, which

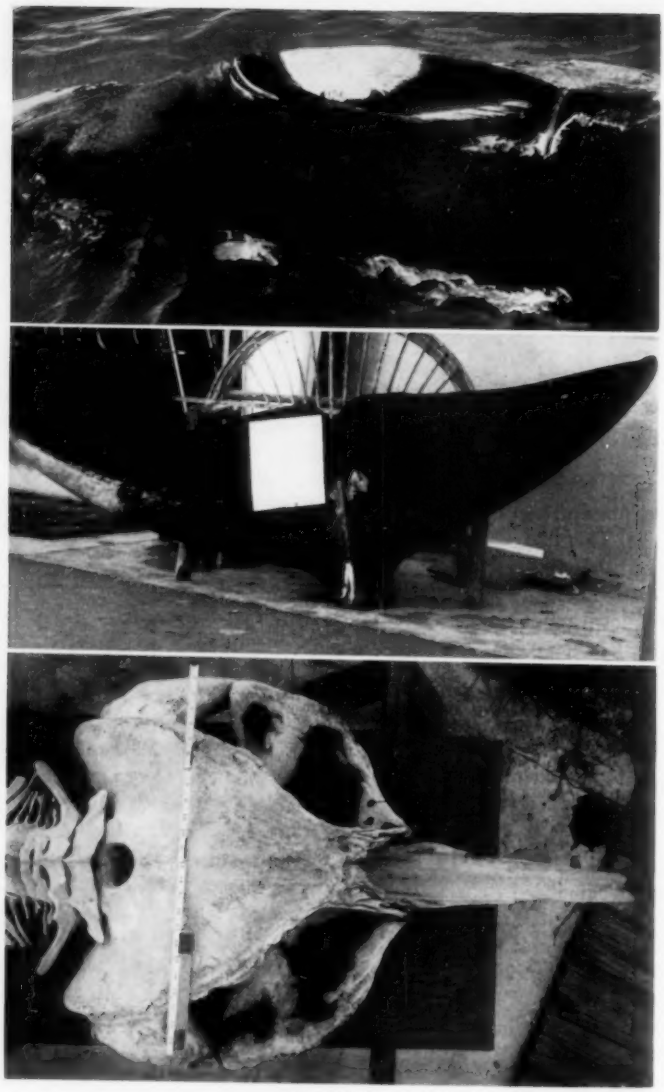

PLATE I

UPPER: Little Duck Key whale, *Balaenoptera acutorostrata*. The right flipper shows characteristic white spot or band identifying this species. There was no abrasion or cutting on the flipper itself. The white of the animal's belly may be seen to extend up under the flipper. Whale's head is toward reader's left. MIDDLE: Dorsal view of flukes of Little Duck Key whale. Greater abrasion of right fluke suggests that whale stranded on right side first, struggled less after turning over on left side. LOWER: Dorsal view of skull of Bahia Honda Key whale, *Balaenoptera acutorostrata*. Maxillary, intermaxillary, and nasal bones have been broken away.

was exposed and undamaged, identified the whale as a little piked whale by the the large white band upon its outer surface.

This whale had been observed by local fishermen to strand itself on the bar on December 28, in pursuit of a school of fish, they thought; and as it lay thrashing there, one of them had killed it with a gun. Many people had visited it from Marathon by boat, and its tail had been cut off and exhibited in front of Brantner's sporting goods shop. We had already photographed and examined the tail there, finding the total width of it to be 89½ inches, the lateral extension of the left fluke being 1½ inches greater than that of the right. The whale was said to have been 30 feet long before the tail was removed. The span of the flukes, however, corresponds closely to that of a 27-foot piked whale from Puget Sound and a 28′ 4″ one from Scotland (Cowan, 1939).

On this same visit to the Florida Keys, the authors found the skeleton of a small whalebone whale on exhibit at the charter boat docks at Marathon. We photographed it and made some inquiries about it, but its owner was out fishing. A month later the senior author returned to the Seven Mile Bridge site by a boat kindly arranged for by Mr. Ike Sigler of Marathon, to search the bar thoroughly but vainly for the stranded piked whale's skull. On this occasion the owner of the exhibited, dockside skeleton at Marathon was on hand. This was charterboatman Ed. H. Lowe of Marathon, who said he had found this whale skeleton in two feet of water off a protected inlet on Bahia Honda Key (lat. 24° 30′, long. 81°17′) in 1952. There were bullet holes in the skull which he said were there when he found it. He had the seven cervical vertebrae and 29 other vertebrae joined to the skull on a steel rod. I measured what he had assembled and, carefully estimating for the missing beak and flukes, judged the whale to have been about 20 feet long at death. The sutures of the skull were largely open, and the epiphyses were not fused to the vertebrae, indicating that the animal was immature.

Lowe was interested in what he could learn about his whale skeleton, and was very obliging. He permitted removal of the tympanic bones for presentation to the United States National Museum in his name, and directed me to his house where I could find and measure the mandible. The following table shows how the available measurements of this 20-foot whale compare with those of two 18-foot piked whales from Scotland (True, 1904). This and the size of the animal, the size and shape of the available portion of its skull, and the shape of its tympanic bones, convinced us that we were again dealing with the little piked whale, *Balaenoptera acutorostrata*.

Jonsgaard (1951) has remarked upon the scarcity of records of the little piked whale in tropical waters, mentioning only a report of one captured in January, 1925, in Manila Bay of the Philippine Islands (lat. 14° N.), which event was apparently regarded (locally?) as extraordinary. There is also a report by Deraniyagala (1948) of a 21-foot specimen stranded at Mannar to the northwest of Ceylon (lat. 10° N.) possibly in May of 1937 since a local newspaper published a photograph of it May 19.

Jonsgaard (*op. cit.*) has concluded from good evidence that piked whales "migrate into Norwegian and [nearby] Arctic waters in the spring, are most

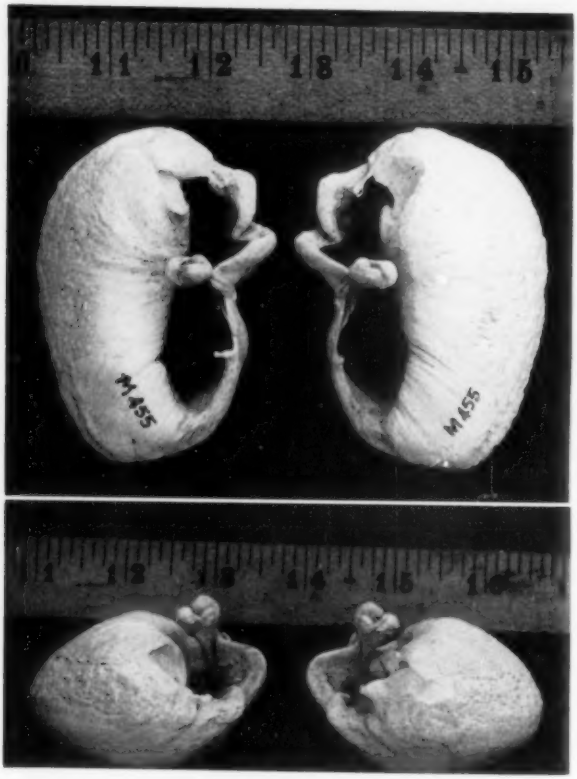

PLATE II

UPPER: Dorsal view of tympanic bones of Bahia Honda Key whale, *Balaenoptera acutorostrata*. LOWER: Posterior view of same tympanic bones. The bones are placed in an unnatural relationship to each other, for the one on the reader's left is the animal's right tympanic bone.

TABLE 1.—*Comparison of Bahia Honda piked whale with Scottish ones*

Measurements	Bahia Honda	Elie	Burntisland
Length of animal (in feet)	20?	18	18
Greatest breadth of skull (in mm.)	679	584	584
(In % of breadth of skull)			
Foramen magnum to top of occiput	53.9	54.3	56.5
Length of mandible (straight)	208.0	186.5	197.5
Height of mandible at condyle	18.7	20.8	19.5
Height, mandible at coronoid process	24.6	23.9	24.7
Height, mandible at symphysis	11.2	10.0	8.7

frequent in the summer, and leave these northern waters again (more or less completely) in the autumn." With specific reference to Norwegian coastal waters, he further concludes ". . . the adult minke [piked] whales met with in Norwegian coastal waters (Lofoten) are en route, migrating towards higher latitudes, where they tend to stop for some time in the summer . . . These animals pass through the Norwegian coastal waters a second time on their way back to temperate waters where they probably spend the winter."

Fraser (1953) compares a summary of the strandings of the little piked whale on British coasts with Jonsgaard's (*op. cit.*) report and concludes that, "In general, the sequence of events off the Norwegian coast would appear to have its counterpart in British waters, taking into account the positions of the two regions on the migration route, and making allowance for the nature of the information available about the [piked whale] in British waters." Since Jonsgaard implies that the whale may winter in temperate waters, and Fraser (*loc. cit.*) shows records of strandings on British shores (lat. 50° to 60° N.) in November, January, and February, one wonders how far south the bulk of the migrants may move.

The small area of Arctic waters compared with the vastness of temperate and tropical waters makes possible such a wide dispersal of piked whales in winter as to minimize notice of them and to cause this whale to be regarded as rare in temperate and tropical waters. Scarcity of biologists in the tropics would further minimize reports from there. The two known dates of strandings of this whale at its southernmost known locale in the North Atlantic, the Florida Keys, are winter dates, mid-February 1949, and December 28, 1953. If there is a seasonal migration of this species on the American side of the North Atlantic, which corresponds to that described by Jonsgaard (*op. cit.*) and Fraser (*op. cit.*) for the European side, the Florida records may reasonably be offered as evidence that migrating individuals have on four occasions reached at least as far south as the 25th parallel.

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SPECIATION IN THE MONA MONKEYS

By A. H. Booth

In the course of investigations started in June, 1952, on the biology of the Gold Coast monkeys, the writer has made an attempt to plot the geographic distribution and limits of all the forms that include that country in their range. The results obtained indicate that the commonly accepted nomenclature of certain forms within the genera *Cercocebus*, *Cercopithecus* and *Colobus* fails to give a true picture of their specific or infraspecific status. The present investigations on the mona monkeys in the field have been sufficiently interesting to lead to a systematic study of the treatment of the entire mona group, *Cercopithecus mona* subspp. of Schwarz (1928*a*, *b*).

Ideally, to gain an accurate idea of specific and subspecific differences, a single worker should study a group of related forms in their natural environment over the whole of their range. Such an opportunity rarely occurs in Africa, and it usually becomes necessary to apply what knowledge can be gained over a portion of the range to the group as a whole. Although the writer has been able to study only two of the eleven recognised forms of mona monkey in the field, he has found himself particularly fortunately placed geographically for the observation of species differentiation. The idea of species-structure thus formed would seem to be confirmed by supplementary museum work.

Material.—Observations and collections of the forms *Cercopithecus mona* (Schreber) and of *C. campbelli lowei* Thomas have been made by the writer between Togoland in the East, and Guiglo, Ivory Coast, in the West. This area contains a belt of forest about six hundred miles long in which these monkeys are common. In addition, some scores of specimens have been kept in captivity in the Department of Zoology, University College of the Gold Coast, both for observation and as experimental material.

The skins and skulls comprising the material in the British Museum (Natural History) have also been examined. There is in the Museum adequate material of the following forms (the nomenclature adopted is that of the original descriptions): *C. campbelli* Waterhouse, *C. campbelli lowei* Thomas, *C. mona* (Schreber), *C. denti* Thomas, *C. pogonias* Bennett, *C. grayi* Fraser, and *C. wolfi* Meyer.

The writer regrets that he has been unable to examine series of the following: *C. nigripes* du Chaillu, *C. mona schwarzianus* Schouteden, *C. elegans* Dubois & Matschie, and *C. pyrogaster* Lönnberg. For confirmation of the validity of these forms, he has relied on the work of Schouteden (1947) and of Malbrant and Maclatchy (1949).

EARLIER TREATMENTS OF THE GROUP

It was decided to include a section on this aspect of the subject because of its wide application to the present state of the classification of African monkeys in general. Failing adequate analysis of skull-characters (Haddow, 1952), divisions of the genus *Cercopithecus* have been made mainly on the basis of differences in

pelage. Such a wealth of forms is known, however, that earlier workers, whose material was often confined to trade skins and specimens that died in captivity, were inclined to choose unfortunate characters for their diagnoses.

Menagerie specimens, when alive, can be extremely useful, especially from the point of view of the investigator who is interested in voice, posture, behaviour and facial expression, all of which are good indicators of relationship, if less susceptible than the pelage to succinct description. The present group furnishes a good example. Sclater (1893), in his revision of the genus, placed *C. campbelli* and *C. mona* in his highly artificial group, the *Cercopitheci melanochiri*. *C. grayi* was placed in the group *auriculati*, and, indeed, it does differ widely in colouration from the first two forms. When an illiterate African animal attendant was shown a photograph of *C. grayi*, he at once identified it by its facial expression and posture as a mona monkey, although he is familiar only with the local forms. On the other hand, in matters of pelage, menagerie material can be very misleading. Specimens of *C. campbelli lowei*, kept under less than adequate conditions, often come to resemble very closely the nominate forms of *C. campbelli*.

The revision of Pocock (1907) was, except in one respect, the most successful treatment the group has had to date. He acknowledged the work of Pousargues (1896), to whom he gives the credit for realising that *C. campbelli* and *C. mona* belong together with Sclater's *auriculati*. He made one unfortunate mistake with *C. lowei* (*C. campbelli lowei*), which he recognised as distinct, but which he assigned to *C. burnetti* Gray, which is a synonym of *C. campbelli* Waterhouse. With less excuse, Elliot (1913) followed Pocock in this error. Although he claimed to have examined the type, his description of it is clearly one of a specimen of *C. c. lowei*. In fact, *C. burnetti* was relegated to *C. campbelli* by Gray himself (1868), and it agrees with specimens of *C. campbelli* in every respect.

Schwarz (1928*a*) revised the entire genus in a manner consistent with his views on the nature of the species. These views are made clear in his (1928*b*) paper on species formation in the mona monkeys. In view of the state of our knowledge at the time, this was a highly important contribution, containing a most careful analysis of the possible interrelationships of the known forms of mona monkey. Schwarz concluded that the various forms, all of which he described as subspecies of *Cercopithecus mona*, although of differing morphological, genetic and evolutionary "value," "gehören alle noch einer Art (Formenkreis) an." It is in this last sentence that we see the whole background of Schwarz's mammalogical researches. Forms that are closely related, and that approximately replace each other geographically, belong, in his opinion, regardless of biological considerations, to a single species.

The recent tendency has been to take the nomenclature of Schwarz as a basis, and to superimpose alterations where the investigator has disagreed. Thus Rode (1937) accepted Schwarz's classification of the spot-nosed monkeys (albeit with a characteristic suppression of many valid races), but disagreed with him in the case of the monas, which had actually been treated much more carefully by Schwarz. Both Schouteden (1947) and Haddow (1952), on the other hand, though disagreeing with Schwarz on the spot-nosed monkeys, made no comment

upon his treatment of the mona monkeys. It is evident, therefore, that there is a need for a new regrouping of the species of the genus.

Three "sections" of the "species" *C. mona* were recognised on morphological grounds by Schwarz:

a. *mona*-section: *campbelli*, *lowei*, *mona*.
b. *pogonias*-section: *pogonias*, *grayi*, *nigripes*.
c. *wolfi*-section: *wolfi*, *pyrogaster*, *elegans*, *denti*.

The *mona*-section was characterised by the greater area of unpigmented skin on the lips and face, by the plain dark grey colour of the outer thighs, by the even distribution of hair on the tail, and by the presence of black annulations on the hairs of the ear-tufts. In addition, a skull-character was discovered. In the males of the *mona*-section, the face was held to be longer, and the premaxillary region narrower than in the *wolfi*- and *pogonias*-sections.

The *pogonias*-section was distinguished from the *wolfi*-section by the development of a sagittal hair crest and the smaller size of animals of the *wolfi*-section. On the other hand, the two sections were alike in the smaller area of unpigmented skin on the face, in the tendency to develop longer and thicker fur towards the distal end of the tail, in the absence of annulations on the hairs of the ear-tufts, and in the development to varying degrees of red pigmentation on the under surface. The shape of the skull in the male was also considered to be more rounded and hence more primitive. Schwarz concluded that the *wolfi*-section contained the most primitive members of the entire group.

After a careful examination of the material at his disposal, the present writer finds himself only partially in agreement with Schwarz concerning the above distinctions. The skull character could, given sufficient material, be subjected to quantitative analysis. The writer would merely record that in the first place he has been unable to detect any overall differences in the male skulls, and in the second place that Schwarz's analysis of monkey skulls has been previously subjected to the same kind of criticism (Haddow, 1952). There is a great degree of variation encountered in skulls within the *mona*-section.

The unpigmented area on the face is subject to a certain amount of variation. Once again, the writer is unable to find any significant degree of difference as between *C. mona* and *C. denti*, although it does appear from the preserved material that *C. pogonias* and *C. grayi* have a little less unpigmented skin. Attention is drawn at this point to Lhoest's photograph in Schouteden (1947) of a live specimen of *C. denti*, which, showing as it does only the head and chest, the writer is quite unable to distinguish from *C. mona*.

The importance of the plain dark-grey thighs of the *mona*-section is very small. A specimen of *C. lowei* shot by the writer in the Ivory Coast is atypical in this respect, in that the outer surface of the thighs is speckled in the same way as the back.

The hair length on the tail of well-grown specimens of *C. lowei* and of *C. mona* is certainly not evenly distributed, those hairs at the end of the tail being from two to four times the length of those at the base. Although the tufted appearance is not developed to such a degree as in *C. pogonias*, the possibility of such a

development is clearly present. Finally, the annulated hairs of the ear-tufts are, undoubtedly, well-marked in *C. mona*, but not so in *C. lowei*. The latter form has black annulations on some of the hairs, but many are only black at the tips, and a considerable number are quite unmarked, the whitish base of the hair blending gradually with the golden-yellow of the tip.

It is therefore concluded that the sharp distinction that Schwarz erected between the *mona*-section and the remainder is not of such morphological importance as he believed.

OVERLAPS IN DISTRIBUTION

Schwarz's distribution map has been brought up to date by the addition of Schouteden's Congo data and of the writer's own data from West Africa. It will be observed (Fig. 1) that there are now two known cases of overlap in range. The first of these was interpreted by Schwarz as follows (italics inserted by the writer): ". . . im Grenzeland des Kamerunberges zwei Lokalformen der gleichen Art, *C. m. mona* and *C. m. pogonias* nebeneinander gefunden worden, die durch Isolierung *weit genug* modifiziert sind, besonders in der Färbung, um *sich nicht mehr zu vermischen*, aber noch nicht weit genug voneinander entfernt, um als ausgetrennte Arten aufgefasst zu werden." It appears in fact that almost the entire range of *C. pogonias* is also occupied by *C. mona*.

The other case of overlap was not known to Schwarz. He remarked on the possibility of speciation between *C. mona* and *C. lowei* in the area of the Togo-Dahomey Gap, a substantial break in the forest belt that stretches from the Volta to the western border of Nigeria. *C. mona* has occupied the small tracts of forest that occur within this gap. With it there also occur other Nigerian mammals. *Funisciurus auriculatus* is an example. A greater number of the mammals of these forests are, however, western types. Examples among the monkeys are *Colobus polykomos vellerosus*, *Cercopithecus petaurista petaurista* and *Procolobus verus*. *C. lowei* is not found east of the Volta. *C. mona* has, however, penetrated further, and extended its range into that of *C. lowei*, particularly along the Afram River and the western bank of the Volta, where the two forms overlap. Fig. 2 shows the extent of this invasion so far as it has been possible to investigate it.

Expeditions by the writer to this area have afforded the following observations:

(1) Local hunters recognise the two forms and assert that they can always tell the difference. In the area of the Afram river, *C. lowei* is known by the familiar Akan name *okwakuo*, and *C. mona* as *apanhen*.

(2) Although the two forms have been seen separately many times, the author and his assistant have only twice seen mixed troops. In both cases the troops were abnormally large, being presumably chance aggregations at an unusually good source of food. Such aggregations occur between almost any two species of forest monkey, were frequently recorded by Haddow (1952) in Uganda, and are to be regarded as quite normal, and not necessarily showing any attempt to interbreed.

(3) There are distinct vocal differences between the two forms. Observations

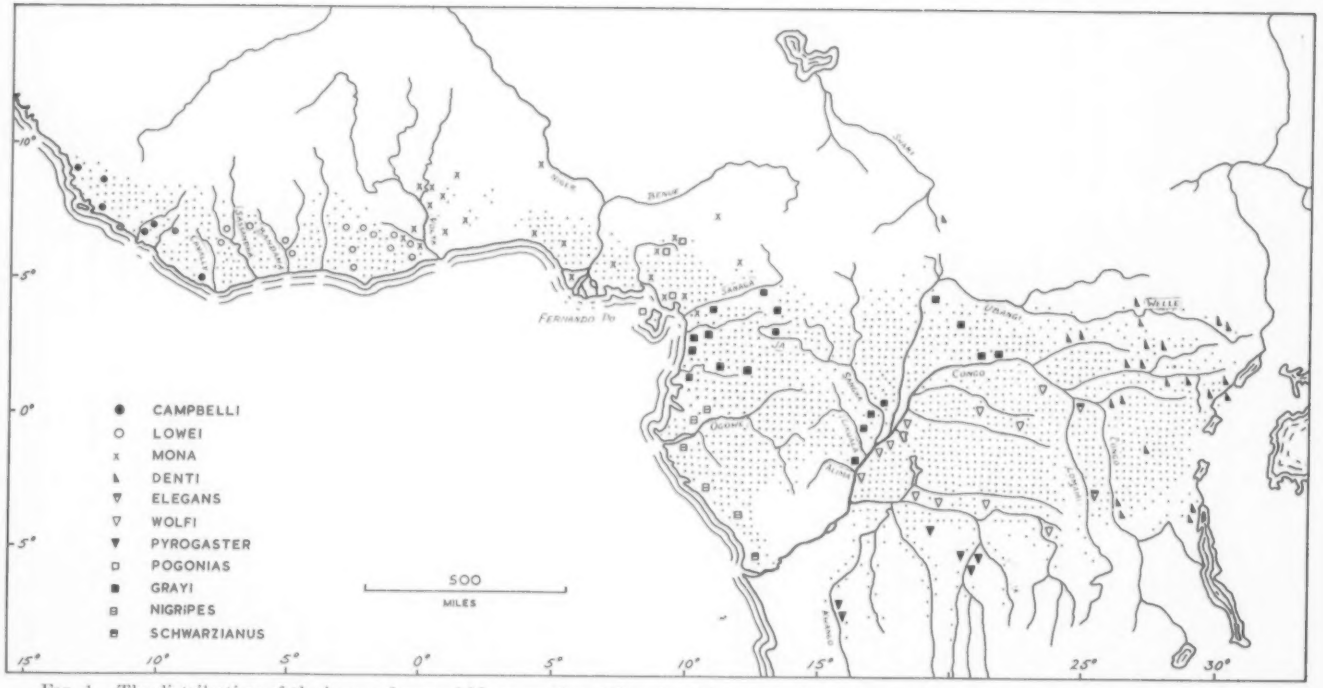

FIG. 1.—The distribution of the known forms of Mona monkey. The stippled areas indicate the extent of the equatorial forest belt. West African Coast from Sierra Leone to Angola.

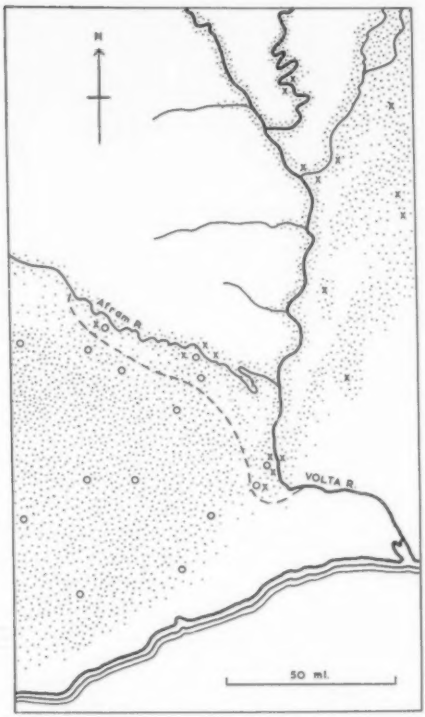

FIG. 2.—The overlap between *C. mona* and *C. lowei*. The known area of overlap is marked with a broken line. The symbols are the same as in Fig. 1. Each symbol represents one observation or specimen, except near the river banks, where the number of observations is too great to be recorded. Gold Coast Region.

and recordings of the calls uttered when feeding and exploring show that while the structure of the utterances is generally similar, those of *C. mona* are invariably harsher and less musical than those of *C. lowei*. For example, the musical call "uíù" of *C. lowei*, which is frequently uttered and may have a significance in holding the troop together, is identifiable in *C. mona*, but sounds rather like a protesting iron hinge. Those barks of the males that are uttered in early morning and late evening are similar. But whereas *C. lowei* troop-leaders utter the same bark when leading a retreat, namely a disyllabic "uáhù," *C. mona* omits the second syllable thus "ué."

(4) Ecologically, in areas where there is no overlap, the two forms are approximately equivalent. In the area of overlap, it would seem that there is a slight difference. *C. mona*, although scattered generally, is distinctly more abundant than *C. lowei* on the actual river banks. There is, in fact, only a single observation by the writer of *C. lowei* on the bank itself, in this case the right bank of the

Volta. At a distance of some few hundred yards from the rivers, however, either form may be encountered. The invaders would seem to have been partially successful in driving *C. lowei* away from the river banks. It is assumed that this initial success is due to the fact that a great deal of the forest in Togoland is in fact riverain, and therefore that monkeys coming from that country would have a preference, if only a psychological one, for such localities.

(5) There is absolutely no evidence from skins or from live specimens from localities in or around the area of overlap that any interbreeding does take place, or has ever done so. *C. lowei* remains identical with more westerly specimens, and *C. mona*, while lighter in colour than Nigerian specimens, is exactly the same on both sides of the Volta. This lightening of pelage was observed by Schwarz in his Togoland material, and was ascribed by him to climatic factors, the Togoland forests being less dense than those of Nigeria. In the writer's view, this is correct. It should be noted that thereby *C. mona* actually becomes less like *C. lowei* as it approaches the area of overlap, since *C. lowei* is in fact darker over the thighs than typical *C. mona*.

The morphological differences between the two forms are as follows:

(1) *C. mona* possesses a white frontal band, absent in *C. lowei*.

(2) The crown as far as the back of the neck in *C. mona* is lightly flecked with a pale lemon yellow. This flecking is produced by the presence of yellow annulations on the black hairs. In *C. lowei* the crown is much more heavily flecked with a rich golden yellow, which merges gradually with the colour of the back.

(3) The back in the adult *C. mona* contrasts with the head in colour, being a warm red-brown. In *C. lowei*, the golden colour of the head speckling becomes a red-gold on the shoulders and thorax, which fades over the lumbar and sacral regions to a dull black. The effect of the colouration of the back in *C. lowei* is golden-reddish or golden-greenish according to the light. In *C. mona* the brown element is always apparent in post-juvenile phases.

(4) The outer thighs of *C. mona* are slate grey as compared to the dull black of *C. lowei*.

(5) *C. mona* has two conspicuous white spots, one at either side of the root of the tail. These are unique in the entire genus.

It is obvious that of the two forms, it is *C. mona* that has the prominent characters. Their biological value may safely be assumed to be recognition, and indeed both the white brow-band and the white sacral spots are clearly visible in the field. It is feasible that they have played an important role in the prevention of any attempt to interbreed with *C. lowei*.

These two forms have, then, diverged in colouration, in voice, and perhaps in other physiological and ethological characters sufficiently to obviate interbreeding in the natural environment, just as Schwarz admitted to be the case between *C. mona* and *C. pogonias*.

Under the circumstances, the writer suggests a regrouping of the *mona* monkeys on the basis of the species definition given by Mayr (1940): "A species consists of a group of populations which replace each other geographically or ecologically, and of which the neighbouring ones intergrade or interbreed wherever they are

in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographic or ecological barriers." Where geographic barriers are present, whether the two races on either side are not conspecific ". . . can be decided only by inference, based on a careful analysis of the morphological differences of the compared forms" (Mayr, 1942).

PROPOSED REGROUPING OF SPECIES

By the adoption of Mayr's definition of the species, the writer commits himself to recognising *C. mona* and *C. campbelli lowei* as specifically distinct, and similarly *C. mona* and *C. pogonias*. On the basis of morphological differences, the isolated southern Congo forms, *C. wolfi* and its relatives, will also be shown to merit specific separation, and, although with less certainty, *C. denti*. The analysis of the group follows.

Cercopithecus campbelli Waterhouse.—Range: French Guinea to the Volta River, Gold Coast.

Cercopithecus campbelli campbelli Waterhouse.—Type from Sierra Leone. Range, French Guinea to Cavally River, Liberia.

Cercopithecus campbelli lowei Thomas.—Type from Bandama, Ivory Coast. Range, Cavally River to Volta River.

The furthest eastward record of the nominate race is Fort Binger, Cavally River. The writer has collected two examples at Guiglo, Ivory Coast, which he has assigned to *C. c. lowei*, although they are somewhat atypical.

CCL 11, female, subadult, has the thighs and sacral area speckled only slightly, less strongly than the more anterior portion of the back.

CCL 10, male, subadult, has a small white brow-band, not so prominent as in the typical race, but much more so than in typical specimens of *C. c. lowei*. It is confined to the middle of the forehead only.

The abnormality in CCL 11 is quite remarkable. The specimen was in other respects normal, healthy and almost fully grown. Perhaps the best explanation of both these variants is the presence of a degree of genetic instability due to interbreeding as the two races approach each other geographically. Guiglo is less than forty miles from the Cavally River. Intergradation is in this case not proven, but may reasonably be inferred.

Cercopithecus mona (Schreber).—Type locality unknown. Range: from Kwahu State, Gold Coast, to Edea, Sanaga River, Cameroons.

This species must be regarded as monotypic, unless the Togoland form proves to be sufficiently stable to be separated as a new subspecies.

Cercopithecus pogonias Bennett.—Range: Fernando Po and Cameroons southward to the Congo River and eastward across the Ubangi River to the edge of the Stanleyville District, Belgian Congo.

Cercopithecus pogonias pogonias Bennett.—Type probably from Fernando Po. Range, British Cameroons south to the Sanaga River.

Cercopithecus pogonias grayi Fraser.—Type locality unknown. Range, from the Sanaga River and Spanish Guinea via the Ja River into the northern half

of the Congo basin. Recorded from the Alima-Sangha-Likouala system of tributaries (Malbrant and Maclatchy), and along the north bank of the Congo as far as the edge of the Stanleyville District. In this eastward part of the range, and Ubangi River forms its northern limit (Schouteden).

Cercopithecus pogonias nigripes du Chaillu.—Type from Gaboon. Range, Gaboon and western Middle Congo (Malbrant and Maclatchy). Apparently the distribution of this form is centred on the Ogowe River and its tributaries.

Cercopithecus pogonias schwarzianus Schouteden.—Type and only specimen from Mayumbe, a small "peninsula" of forest just north of the mouths of the Congo.

This wide-ranging species has had a variety of different treatments, as will be seen from Table 1. This is the result of the frequent occurrence of individual variants and of intermediates. Rode characteristically refused to recognise any of the well-marked races as distinct. *C. p. pallidus* Elliot and *C. petronellae* Büttikofer were relegated by Schwarz to the synonymy of *C. p. grayi*. Apart from the recent addition of *C. p. schwarzianus* by Schouteden on the basis of a single captive specimen, the writer has nothing further to add to Schwarz's account. It is urgently necessary to assemble in one place a large collection from all parts of the range of *C. pogonias* before this remarkably variable species can be adequately surveyed.

Cercopithecus wolfi Meyer.—Range: The whole of the forested area on the left bank of the Congo and its tributaries.

Cercopithecus wolfi wolfi Meyer.—Type locality unknown. Range, between the Lomami and Kasai rivers.

Cercopithecus wolfi pyrogaster Lönnberg.—Type from Kwango River. Range, from Kasai to Kwango rivers.

Cercopithecus wolfi elegans Dubois & Matschie.—Type from Lower Lomami River (Schouteden). Range, between Lomami and Congo rivers.

These three forms have been regarded by all authorities since Schwarz's revision as geographic races of *C. mona*. From this form the writer regards them as specifically distinct on morphological grounds. The major differences in pelage are as follows:

(1) The brow-band is extremely well-marked, and stretches round to a point above the ears. In *C. mona* it tends to blend gradually with the colour of the crown, and fades over the temples, considerably anterior to the ears.

(2) There is a clean line between the pigments of the upper and lower surfaces, emphasised by a darkening of the flanks at the junction between the grey upper pigments and the orange or white lower. In *C. mona*, the colours merge gradually.

(3) The colour of the thighs is sharply marked off from the colour of the sacral area. This is not the case in any other species in the group.

(4) There are no white spots at the base of the tail.

From *C. pogonias*, *C. wolfi* is separated by characters 1, 2 and 3 above, and also by the failure to develop any indication of a sagittal hair crest.

The degree of difference between the forms assigned to *C. wolfi* and the races of *C. pogonias* is therefore considered to be sufficient to warrant specific distinc-

TABLE 1.—*Nomenclature of monkeys of the mona group of the genus Cercopithecus*

Describer's name	Sclater 1893	Pocock 1907	Elliot 1913	Schwarz 1928	Rode 1937	Present revision
mona; Schreber, 1774	*mona*	*mona*	*mona*	*m. mona*	*m. mona*	*mona*
campbelli; Waterhouse, 1838	*campbelli*	*campbelli*	*campbelli*	*m. campbelli*	*m. campbelli*	*c. campbelli*
burnetti; Gray, 1842	*campbelli*	—	*burnetti*	*m. campbelli*	*m. campbelli*	*c. campbelli*
c. lowei; Thomas, 1923	—	*burnetti*	*burnetti*	*m. lowei*	*m. campbelli*	*c. lowei*
denti; Thomas, 1907	—	*denti*	*denti*	*m. denti*	*m. denti*	*denti*
wolfi; Meyer, 1891	*wolfi*	*wolfi*	*wolfi*	*m. wolfi*	*m. wolfi*	*w. wolfi*
elegans; Dubois & Matschie, 1912	—	—	—	*m. elegans*	—	*w. elegans*
pyrogaster; Lönnberg, 1919	—	—	—	*m. pyrogaster*	—	*w. pyrogaster*
pogonias; Bennett, 1833	*pogonias*	*pogonias*	*p. pogonias*	*m. pogonias*	*pogonias*	*p. pogonias*
nigripes; du Chaillu, 1860	*nigripes*	*g. nigripes*	*p. nigripes*	*m. nigripes*	*pogonias*	*p. nigripes*
grayi; Fraser, 1850	—	*g. grayi*	*g. grayi*	*m. grayi*	*pogonias*	*p. grayi*
erxlebenii; Dallbet & Pucheran, 1856	*erxlebenii*	*g. grayi*	*g. grayi*	*m. grayi*	*pogonias*	*p. grayi*
pallidus; Elliot, 1909	—	—	*g. pallidus*	*m. grayi*	*pogonias*	*p. grayi*
petronellae; Buttikofer, 1911	—	—	*petronellae*	*m. grayi*	—	*p. grayi*
m. schwarzianus; Schouteden, 1944	—	—	—	—	—	*p. schwarzianus*

tion. As compared with *C. mona*, *C. wolfi* is further separated by distance and presumably by a considerable period of time during which their evolution has proceeded independently.

C. w. elegans, of which there still exist only five preserved specimens, is a most interesting form, in that the orange pigment developed to such a degree in *C. w. wolfi*, and more especially in *C. w. pyrogaster*, has failed to appear. It therefore forms a good connecting link with the next species. The variations in the races of *C. wolfi* at their common limits is not reported. Since the differences are largely confined to the intensity of pigmentation, as opposed to differences in pattern, the writer follows Schwarz in regarding them all as of subspecific value.

Cercopithecus denti Thomas.—Type from Ituri Forest, eastern Belgian Congo. Range: The right bank of the Congo to Stanleyville. Eastward to the Rift Valley and northward across the Ubangi to M'Bres, Ubangi-Shari (Malbrant, 1952).

This species is almost exactly intermediate in form between *C. mona* and *C. w. elegans*. From the former it is separated by about five hundred miles of unfavourable country, and from the latter by the upper reaches of the Congo. It is therefore the most difficult member of the whole group to assess. The dorsal surface is almost indistinguishable in colour from that of *C. mona*, except that the prominent white spots at the root of the tail in that form are absent in *C. denti*. The crown and brow-band are almost identical, although the brow-band is if anything less pronounced in *C. denti*. In side view, however, there is a considerable difference. *C. denti* has the sharp demarcation of the flanks from the belly which has been noted in *C. wolfi*. The outer surface of the thighs is speckled olive brown, and blends much more gradually with the colour of the sacral area.

From *C. w. elegans*, the main differences are in the crown-pattern, which is very distinctive in all the forms of *C. wolfi*, in the lack of a sharp demarcation of the colour of the thighs from that of the sacral area, and in the darkening of the cheek hairs; these hairs, in *C. w. elegans*, are in the anterior region of the cheek markedly light in colour. Together with the brow-band, they give this form a quite characteristic pattern of head-markings, well shown in the photograph of the type, accompanying the description by Dubois & Matschie (1912).

The writer's conclusion that this form is specifically distinct from *C. wolfi* is finally influenced by Schwarz's admission that it stands in a somewhat isolated position in his *wolfi*-section. There is no doubt that it is distinct from *C. mona*, despite the resemblance in the colour of the dorsal surface and crown-pattern, which Schwarz failed to remark.

INTERRELATIONSHIPS OF THE SPECIES

Since the writer regards Schwarz's craniological evidence of the advanced state of his *mona*-section as inconclusive, this discussion will be concerned only with the evidence of the pelage. There is little doubt that smooth gradations in pattern and sombre colours are to be regarded as more primitive than contrasting

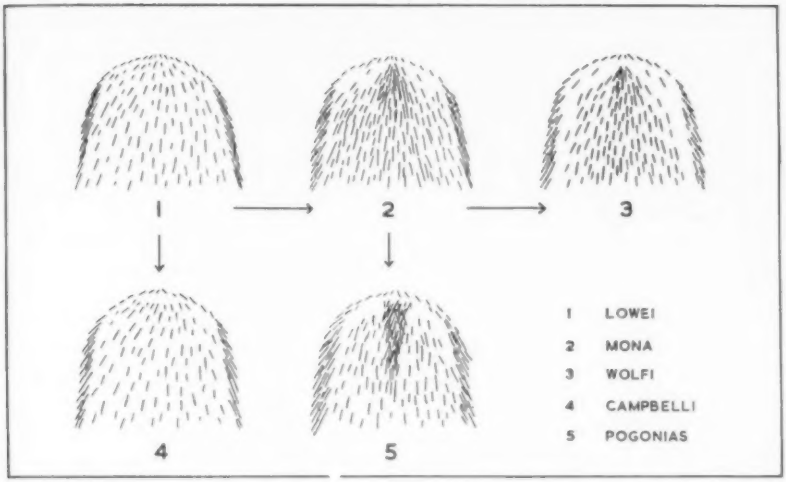

FIG. 3.—The crown patterns in various forms of Mona monkey. The arrows indicate the supposed evolution of the crown pattern.

patterns and bright colours. In the course of the differentiation and spread of a species, recognition marks are more likely to be acquired than lost. On this assumption only *C. c. lowei* can be regarded as of primitive colouration and pattern.

It is evident from an examination of the colour patterns over the whole group that we have here a beautiful example of a very ancient cline, which, owing to periods of advance and retreat of forest vegetation under the influence of climatic factors, has become differentiated into species. The gradations in pattern of the brow-band are illustrated diagrammatically in Fig. 3. The isolated position of *C. pogonias* will be dealt with later. The forms *lowei*, *mona*, *denti*, *elegans*, *wolfi*, and *pyrogaster* are, in almost every respect, a graded series.

Dorsal surface and outer hind limb.—In *C. c. lowei*, crown golden-yellow speckled, becoming red-gold on the thoracic region, fading to dull black on the sacral region and over the outer thighs. In *C. mona*, crown lightly speckled lemon yellow, contrasting with the back, the red-brown of which fades gradually to plain medium grey over the thighs, darkening on the lower leg. Feet black. In *C. denti*, slightly darker, the speckling continued strongly onto the olive brown thighs, and onto the lower leg, the feet only remaining black. A sharp, sometimes darkened, line of demarcation of the upper surface from the pure white of the belly. In *C. wolfi* subspp., the red-brown of the back confined to the mid-dorsal region, the flanks being of a speckled dark grey colour. A sharp line of demarcation not only of the flanks from the belly, but also of the thighs from the sacral area. In *C. w. elegans*, the hind leg to the ankle a very light speckled yellow-grey; in *C. w. wolfi*, infused with rusty red, and in *C. w. pyrogaster* brilliantly so, the red colour spreading over the whole body.

The under surface.—In *C. c. lowei*, a rather dirty white, especially posteriorly.

In *C. mona*, the throat and chest rather more brilliantly white. In *C. denti*, pure white, and sharply marked off from the upper surface. *C. w. elegans* as *C. denti*. *C. w. wolfi* infused with orange laterally, much more strongly in *C. w. pyrogaster*, in which the red colour extends upwards over the flanks onto the dorsal surface, thus obscuring the demarcation line.

The fore-limbs.—Throughout, jet-black outside, except for the upper region which may be lightly speckled. Inside, pure white except in the erythristic forms *C. w. wolfi* and *C. w. pyrogaster*.

West of *C. c. lowei*, we find in *C. c. campbelli* the indication of a tendency to a parallel set of modifications in the appearance of a small but distinct white brow-band, and in the lighter colour of the outer thighs and sacral area.

C. pogonias the writer believes to be most closely related to *C. mona*. The acquisition of a sagittal hair crest on the head can be understood with reference to the brow-band pattern of *C. mona*. This crest is least developed in *C. p. pogonias*, which is geographically nearest to *C. mona*. No sharp demarcation of the thighs or of the upper surface from the belly has been evolved, though the contrasting ear-tufts have appeared in correlation with the generally erythristic tendencies of the species. There is also a distinct tendency for the arms to be speckled; the hands remain black. On the other hand, *C. pogonias* does not fit in with the cline described above, and has in the writer's opinion undergone a much longer period of independent development.

The apparent relationships of the species and their degree of differentiation may be accounted for by the alternate advance and retreat of the forest in four areas. The first, in the region of Togoland, has already been discussed rather fully. The second is the gap between the main massif of the Cameroons and the coast. *C. mona* and *C. pogonias* have clearly become differentiated as a result of the retreat of the forest from this area over a considerable period of time. It may be supposed that during this time *C. pogonias* spread as far south as the Congo River, and eastward along the right bank. The third area still remains as savannah, separating *C. mona* from *C. denti*. It is suggested that the connection between these two forms may have been via forests which formerly existed along the basin of the Benue River, connected with the Shari and its tributaries to the north of the main Cameroon massif. From Ubangi-Shari, *C. denti* is found eastward and southward along the right bank of the upper Congo. It is most unfortunate that its boundary with *C. p. grayi* is unknown. The fourth area to be considered is that of the upper Congo itself, south of its junction with the Lomami. It is in this region that the writer concludes that the differentiation of *C. wolfi* from *C. denti* took place. It is, even now, an area of transition, the forests being confined mainly to the river basins, and it is easy to see how, once the crossing of the Congo had been made, *C. wolfi* may have had the opportunity to develop in isolation.

The writer therefore disagrees with Schwarz, who saw the origin of the group as somewhere in the Congo basin. It is much more reasonable to suppose that the actual origin was somewhere to the west of the Cameroons, in the region where the forms with the most primitive type of pelage are to be found today.

PLATE I

UPPER: *Cercopithecus campbelli lowei* Thomas. Subadult male. The photograph shows the absence of a contrasting brow-band, and of the white sacral patches. The hind legs are almost as dark in colour as the fore legs.

LOWER: *Cercopithecus mona* (Schreber). Subadult male. The contrasting brow-band and the white sacral patch stand out clearly. The thighs are lighter in colour than in *C. campbelli lowei*. The photograph also shows how *C. mona* approaches *C. pogonias* in crown pattern. From an anterior view, it almost appears as if there might be a black sagittal hair crest.

From this region two main migrations occurred, one to the south of the Cameroons and one to the north.

SUMMARY

The need for a revision of the genus *Cercopithecus* is emphasised, and the earlier work on the *mona* group is examined critically.

Field studies of *C. mona* and *C. campbelli lowei* are described. There is adequate evidence that the two forms are specifically distinct.

C. mona is also considered to be distinct from *C. pogonias* on the grounds of a similar overlap in distribution without interbreeding.

The group is revised on the assumption that the degree of morphological difference between *C. mona* and *C. c. lowei* and between *C. mona* and *C. pogonias* is sufficient to allow specific separation between other forms, the geographic location of which does not permit of overlaps in range. It is concluded that five species are admissible, two of which are monotypic.

The probable course of the evolution and spread of the group is discussed.

ACKNOWLEDGEMENTS

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NOTES ON AMERICAN MONKEYS OF THE GENUS *CEBUS*

BY PHILIP HERSHKOVITZ

Critical remarks by the late Dr. G. H. H. Tate (1954) regarding my identification of *Cebus apella* Linnaeus seem to be founded on a misunderstanding of the significance of certain external characters of the species and a misinterpretation of the terminology used for indicating those characters.

The original figure and description of *Simia apella* Linnaeus, 1766, reproduced by Tate (1954, Pl. 1) refers quite correctly to the animal all authors have held to be *Cebus apella*. My 1949 characterization of *Cebus apella* is based on the same figure as well as on large series of specimens from various museums and others accumulated by Dr. Remington Kellogg for his study of the species *Cebus apella*.

The basis for the difference of opinion is that Tate (1954: 415) points to one animal but holds in mind a totally different one when he states that *C. apella* is "an uncrested species and that the name appeared to be applicable to the common gray-brown species inhabiting the Guiana region, which Hershkovitz (p. 332 [1949]) refers to *C. nigrivittatus castaneus*." Tate goes on to say (p. 417) that comparisons of the picture of the original *C. apella* "with the *apella* of Hershkovitz (1949: 325, Fig. 52) will, I think, forever still any doubt that Linnaeus had before him an uncrested *Cebus* monkey when he described *Simia apella*."

Tate's concept of crested and uncrested species of *Cebus* is based solely on cranial characters and primarily on the presence or absence of a sagittal crest on the skull of the adult male (cf. Tate, 1939: 210). Neither sex nor cranial characters of the original *Simia apella* are placed in evidence. Obviously, Tate confused his own term *crested*, referring to cranial characters, with his and my term, "tufted," referring to a variable external character. It has been shown by me (1949: 326–327, 353, 374, etc.) that hair tufts may be present or absent in any of the four recognized species of *Cebus*. In the *cranially crested* (my "tufted") *Cebus apella*, tufts of hair on the crown of the head are "usually," not always, present and they may appear as "horns, ridges, topknots, pompadours;" they may be represented by a few raised hairs or they may be obsolete. It has been shown by Tate (1939: 209) that presence or absence of hair tufts in his *cranially crested* species is not a critical character. He chided Elliot for including the *cranially crested C. variegatus* and the *cranially crested C. frontatus* in the section "without tufts,"

because he, Elliot, failed to find tufts in the types of the named forms. Tate went on to explain that the "development of hair crests [i. e., tufts] varies to a considerable degree in specimens from southeast Brazil. On the other hand," Tate continued, "the cranial features of all our monkeys (as well as the dark color of their hands, feet and tails) from that region combine to ally them with the tufted [i. e., *cranially crested*] forms." It is not clear why Tate should now point to my published figures of *Cebus apella* with its tufts described as a variable, even ephemeral, character, and then to his reproduction of the original drawing of *Simia apella* Linnaeus without visible tufts, as evidence that the two cannot represent one and the same species.

With all said about tufts and other external characters kept in mind, it will be noted that the original figure and description of *Simia apella* reproduced by Tate, shows all external characters attributed by him, and by me, to his *cranially crested*, my "tufted," species. The hands, feet and tail of the Linnaean animal are described as black, the hairs of the crown appear to be short but erect although this may be an interpretation not required for the diagnosis. In any case, the form of the black crown is quite like that of any number of "tufted" individuals examined by me, by Kellogg (*in litt.*, apropos this article) and by Tate as shown in the above quotation. This Linnaean animal represents the "tufted" species described by me in 1949 (p. 327). Its valid diagnostic characters, clearly shown in both the original figure and my figures of *Cebus apella*, but apparently overlooked by Tate, include the pale, narrow superciliary band contrasting with the black cap, and the dark preauricular bands extending from cap to under chin. Every *Cebus*, *with* or *without* tufts, that exhibits the color pattern described in this paragraph, is a true Linnaean *Cebus apella*. *The skulls of all adult males of such individuals possess a bony sagittal crest* and both sexes exhibit the other cranial characters of my "tufted" group (cf., Hershkovitz, 1949: 326, Pls. 15, 16).

In 1939 (p. 212) Tate arrived at the same conclusion but under a different denomination. He declared that "if, as seems possible, the black crowned Cebi, with or without crests [here hair tufts are meant] are really conspecific, all of the named forms will come under the species *fatuellus* [the name given to his *cranially crested* species and an absolute synonym of *apella*] either as races or as synonyms."

It is indeed a paradox that the combination of diagnostic external characters of the true Linnaean *Cebus apella*, so well revealed by Tate, are not present in the monkeys he identified as *apella*. The Guianan and Venezuelan specimen in the American Museum of Natural History recorded by Tate (1939: 213) under the name *Cebus apella* were examined by me and found to have no relationship to the animal shown by Tate in 1954 to be *Cebus apella*. They are all *cranially uncrested*, i. e., true "untufted," brown monkeys with the wedge-shaped cap of the species variously described as *olivaceus*, *castaneus*, *apiculatus*, "*capucinus* of authors," and described and figured by me (1949: 325–328, 343, 348) under the common earliest valid name *Cebus nigrivittatus* Wagner, 1848. Other specimens of the genus *Cebus* from Colombia (Santa Marta) and western Ecuador, also

identified by Tate (1939: 211) as representatives of *Cebus apella*, proved to be, on my inspection, (1949: 332 and corresponding synonymies) forms of the brown, white-fronted *Cebus albifrons*. More instances of this sort are detailed by me in the place cited.

It is unfortunate that the preparation of his report on the mammals of the Guiana region (1939) left Tate little or no time for careful examination, correct naming, and the taking of accurate measurements of the monkeys he described (cf., Kellogg and Goldman, 1944: 5; Hershkovitz, 1949: 387, 401).

Alongside the figure of the Linnaean *Simia apella*, Tate (1954, Pl. 1) presented a reproduction of the original woodcut drawing of *Simia capucina* Linnaeus. The purpose served by the reproduction of this figure is obscure to me. Perhaps Tate wished to emphasize that in view of statements to the contrary, there "never appears to have been doubt" regarding the identity of *Cebus capucinus*. In 1939 (pp. 210–211), however, Tate commented on the "vague '*capucinus* of authors.' " Tate himself was not clear about it. On page 209 (Tate, 1939) he used the name *hypoleucus*, and on page 211, *nigripectus*, for *capucinus*. For a complete taxonomic history of *capucinus* Linnaeus, 1758, and "*capucinus* of authors," not Linnaeus, the reader is referred to my paper on the subject (1949: 333–349). Supplementary remarks on *Simia hypoleuca* Humboldt are given below.

According to Tate (1954: 415) I "make the geographical range of *apella* Matto [sic] Grosso." I made no formal statement defining the range of *Cebus apella*, having deliberately left this matter to Kellogg (Hershkovitz, 1949, 324). I did note the occurrence of the species in Colombia (p. 324), in Peru (p. 374), in Ecuador (p. 376), in the Guianas and lower Orinoco region (p. 380) and, farther down the same page, Margarita Island. Other parts of the range are indicated in connection with my review of the literature (pp. 329 *et. seq.*). My only reference to Mato Grosso (where the species occurs) is in connection with a listing (p. 327) of the vertebral formulae of two specimens of *Cebus apella* from that locality.

Tate remarks, "Hershkovitz (1949, p. 332) suggests that I should have 'rejected' *apella* . . ." The reader in referring to the page cited will find that I did not use the word in the form or sense quoted. Finally, Tate (1939: 213) "restricted" the type locality of *Cebus apella* to British Guiana. First reviser E. Geoffroy (1812: 109) had already restricted the type region to "La Guyane," i. e., French Guiana. The type locality of *Simia fatuellus* Linnaeus was also determined as "La Guyane," by the same authority (1812: 109–110). This makes *fatuellus* an absolute synonym of *apella*.

ON THE STATUS OF SIMIA HYPOLEUCA HUMBOLDT, 1812

In my work (1949: 354) on monkeys of northern Colombia, it was shown that *Simia hypoleuca* Humboldt was not the same as the black white-fronted *Cebus capucinus* Linnaeus, 1758, but was, rather, a race of the brown white-fronted monkey and should bear the name *Cebus albifrons hypoleucus*. The type, a household pet, was examined by Humboldt in a native's hut near the mouth of the Río Sinú, Bolívar (now Córdoba) Department, northwestern Colombia. This

last was construed as an indication of the type locality, there being no more information on the subject. On a subsequent collecting trip in Colombia, I made special efforts to secure specimens of Humboldt's monkey in the alleged type region. The animal was not found there and it can be stated categorically that no representative of *Cebus albifrons* occurs naturally in Colombia anywhere west of the Río Magdalena-Cauca. This state of affairs nullifies my suggestion (1949: 379) that the western Ecuadorian *Cebus albifrons aequatorialis* Allen "possibly" grades into *hypoleucus* "somewhere along the Pacific coast of Colombia."

In the absence of a known habitat for *Simia hypoleuca* Humboldt, the monkey cannot be identified positively beyond its specific designation. It is proposed, therefore, that the name be disposed of as an unavailable synonym of *Cebus albifrons*.

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GENERAL NOTES

SHORT-TAILED SHREW IN SOUTH DAKOTA

Although Over and Churchill (Mammals of South Dakota, 1945: 7, mimeo.) mention that *Blarina brevicauda brevicauda* is found throughout South Dakota, we can find no records of this shrew actually having been captured in the state. The capture of eleven short-tailed shrews from the vicinity of Vermillion, Clay County, South Dakota, therefore, is of interest.

On August 15, 1954, we trapped two short-tailed shrews in tall grass bordering a field of alfalfa, ½ mile north of Vermillion, and nine specimens along the edge of a cattail marsh, ½ mile west of Vermillion. All eleven were young of the year; five of these were preserved and are in the collections of the authors. Average and extreme external measurements in millimeters of the five specimens (4 males, 1 female) are: total length, 128.5 (123–132); tail, 26.5 (25–29); hind foot, 16.2 (15–17). These specimens are assigned to *Blarina brevicauda brevicauda* Say on the basis of their large size. They closely resemble specimens from two miles northwest of Ashland, Saunders County, Nebraska, approximately 35 miles from the type locality of *B. b. brevicauda*.—JAMES S. FINDLEY AND RICHARD G. VAN GELDER, *Department of Zoology, University of South Dakota, Vermillion, South Dakota and Museum of Natural History, University of Kansas, Lawrence, Kansas.* *Received November 15, 1954.*

SWIMMING ABILITY OF THE LITTLE BROWN BAT

A little brown bat (*Myotis lucifugus lucifugus*) was found in the water of Western Lake Erie near Put-in-Bay on South Bass Island. When discovered it was approximately

200 feet from the shoreline of Gibraltar Island at the location of the Stone Laboratory building. It was first observed at 7:45 PM (E.S.T.), while still light, on June 23, 1954. The bat swam the shortest possible distance to shore with only its head above water and landed on the beach where it was captured. It was nearly exhausted from its long swim and did not struggle when handled. It was found to be a post partum female (determined by Dr. Elizabeth Smith). Unfortunately it perished in captivity before arrangements could be made to band and release it. On Gibraltar Island there were two groups of bats residing during the summer months, one in the attic of the boat house and the other in the attic of the men's dormitory. In some way one of them apparently fell into the lake, but it was able to swim ashore. No other record of this has been found in the literature.—THOMAS J. CRAFT AND RALPH W. DEXTER, *Franz Theodore Stone Institute of Hydrobiology, Put-in-Bay, Ohio. Received September 11, 1954.*

SEMINOLE BAT, *LASIURUS SEMINOLUS*, IN CENTRAL NEW YORK

An adult female Seminole bat, *Lasiurus seminolus* (Rhoads), was collected by Karl Warren, William Werner, Jr., and the writer at Ithaca, Tompkins County, New York on September 2, 1953. It was shot about 7 PM E.S.T. while flying over a small pond situated in an open area that was bordered on three sides by woodland. Red bats (*Lasiurus b. borealis*) and little brown bats (*Myotis l. lucifugus*) were also active in the area at the same time. A total of 21 other bats, including 10 *M. l. lucifugus*, 1 *Lasionycteris noctivagans*, 5 *Eptesicus f. fuscus*, and 5 *L. b. borealis*, were killed at this site during seven evenings in late August and early September; but no additional Seminole bats were taken.

Measurements of the specimen (No. 1165 in the writer's collection) are as follows: total length, 110 mm.; tail, 53 mm.; hind foot, 9 mm.; forearm, 42 mm.; and weight, 13.0 gms. In pelage coloration it agrees closely with examples of *L. seminolus* from Florida, Georgia, Mississippi, and Louisiana but is somewhat more frosted on the dorsum than the average female.

This specimen constitutes the first record of the species from New York and apparently the third from northeastern United States. The present locality is over 150 miles N.N.W. of the two previous records from southeastern Pennsylvania cited by Poole (Jour. Mamm., 13: 162, 1932 and 30: 80, 1949). The fact that the three Seminole bats thus far collected in the North have been taken in the fall (September 2, 12, and October 20) lends support to the suggestion of Hamilton (THE MAMMALS OF EASTERN UNITED STATES, Comstock: 96, 1943) that individuals of this species may wander northward in summer in the manner of certain southern birds.

I am indebted to Colin C. Sanborn, Chicago Natural History Museum, and H. B. Sherman, Department of Biology, University of Florida, for examining the specimen and confirming my initial identification. The latter kindly compared the New York example with a series of *Lasiurus seminolus* from Florida.—JAMES N. LAYNE, *Department of Zoology, Southern Illinois University, Carbondale, Ill. Received September 11, 1954.*

THE SEMINOLE BAT, *LASIURUS SEMINOLUS*, IN NORTH CAROLINA

On September 28, 1916, the late C. S. Brimley captured an adult female Seminole bat, *Lasiurus seminolus* (Rhoads), as it hung among the branches of a small tree in a woods near Raleigh, Wake County, North Carolina. In his annotated list, "The Mammals of North Carolina" (Carolina Tips, Installment No. 5, August, 1944, Elon College, N. C.) Brimley identified the specimen as a hoary bat, *Lasiurus cinereus* Beauvois.

A second North Carolina specimen, also an adult female, was shot by the junior author at Camp Steere, which is located near the city of Charlotte, Mecklenburg County, North Carolina, on August 31, 1949. This was the only bat collected on the above date; however, two red bats, *Lasiurus b. borealis*, and one evening bat, *Nycticeius h. humeralis*, were taken in the same area two nights previously.

The skins and skulls of both specimens were deposited in the collection of North Carolina State College and represent the first known records of the occurrence of *Lasiurus*

seminolus in North Carolina. The two individuals reported from Pennsylvania by Dr. Earl L. Poole (Jour. Mamm., 13: 162, 1932 and 30: 80, 1949) and the two North Carolina specimens are to our knowledge the only representatives of this species taken north of the South Carolina border.

Both North Carolina specimens, mature females, are estimated to be over two years old on the basis of tooth wear. A heavy frosting covers the dorsal portions of both and extends from the nape to the posterior half of the interfemoral membrane. Both are darker than any specimen from a series of six that was taken well within the normal species range. The dorsal pelage on the interfemoral membrane near the base of the tail is Mars Brown (Ridgeway, COLOR STANDARDS AND NOMENCLATURE, 1912). Both are darker than the Lancaster County, Pennsylvania, specimen, which is estimated to be an adult of the year on the basis of tooth wear.

Barkalow (Jour. Mamm., 29: 415–416, 1948) reported a northward expansion of the species' range in Alabama during the spring and summer with a corresponding southward recession during the fall and winter. The transition area between the occupied and unoccupied zones at any one time appears to be quite narrow. This condition may be more apparent than real, although the hypothesis is given some support by the fact that the species occurs commonly along the coastal area of South Carolina as far north as Georgetown, while it is completely absent from all collections of the extreme southeastern coastal area of North Carolina. Repeated efforts to collect this species in southeastern North Carolina have thus far been unsuccessful. To date, all specimens taken north of South Carolina have been collected outside the Coastal Plain either in late summer or in early fall. In view of the relatively well-defined northern limit of the main population, it is believed that the occasional records from far outside the normal species range result from a haphazard movement on the part of a few individuals. Sporadic movements are frequently observed in birds and may well occur in the Seminole bat, *Lasiurus seminolus* (Rhoads).—F. S. BARKALOW, JR. AND DAVID A. ADAMS, *Department of Zoology, North Carolina State College, Raleigh. Received September 15, 1954.*

OCCURRENCE OF THE RED BAT, *LASIURUS BOREALIS*, IN CAVES

The red bat is customarily categorized as a "tree bat", a species selecting trees rather than caves for roosting. We wish to record here the finding of an alive and healthy adult male red bat in Bat Cave, Carter Caves State Park, Carter County, Kentucky, on July 30, 1954. The bat was found hanging by the hind feet from the low ceiling of a side chamber of the cave at least 150 feet from the main entrance during the middle of the afternoon. It was torpid and covered with droplets of condensed moisture. The air temperature at different places within the cave was 54°F. Occurring concurrently in the same cave as the red bat, but not associated with it, were specimens of *Eptesicus*, *Pipistrellus*, and *Myotis*. A day later, in the laboratory, the bat was anesthetized with ether and the following data were recorded: weight, 8.9 gms.; total length, 110 mm.; length of tail, 53 mm.; length of forearm, 39 mm.; number of erythrocytes per mm.^{3} of blood from the jugular vein, 17.63×10^6; number of leucocytes per mm.^{3} of blood from the jugular vein, 1222. On the basis of blood counts for other species of bats (unpublished) these counts for the red bat appear normal. Likewise, examination of the internal organs failed to show any pathology.

It should be noted that in the immediate vicinity of Bat Cave there is an extensive forest of large trees and clearings, and that natural roosting sites in trees surely were available to the specimen found in the cave.

Published information on cave usage by the red bat is largely limited to records of dead specimens and does not provide any clues to the circumstances responsible. Since the occurrence of the red bat in caves is not generally appreciated and since many of the published reports are obscure, a summary may be of interest. Godman (1826) quoted some observations by "Professor Jacob Green" on a large number of bats found in a cavern about 12 miles south of Albany, N. Y., November 1, 1816. Green believed the bats to be "V. Noveboracensis", a species which as described by Godman (1826) is clearly the red

bat. However, Green's observations do not conclusively demonstrate this identification. These observations were later quoted by Merriam (1884). H. Allen (1893) stated that specimens of the red bat have been obtained from a cave near Albany, N. Y., by G. J. Green and that the collection of the Museum of Comparative Zoology contains a specimen which was secured in Short Cave, Kentucky. G. S. Miller, Jr. (1897) recorded a specimen from Marble Cave, Stone County, Missouri. Hahn (1907) reported finding about 200 skulls of this species in Donaldson Cave, Indiana, and stated that W. S. Blatchley had informed him that in Wyandotte Cave, Indiana, the ratio of *Lasiurus borealis* to *Myotis lucifugus* is 1:1000. Hall's (1923) report of this species in caves at Atwood, Kansas, was later retracted (Cockrum, 1952). Bailey (1928) found two skulls on the floor of the deepest room in Carlsbad Caverns. Hardy (1941) reported finding two specimens on the walls of the Kenilworth Mine, Carbon County, Utah, September 17, not far from the entrance. Charles Mohr (1952) reported finding a "complete" but dead female in Nickajack Cave, Shellmound, Tennessee, and published a photograph of the specimen. And most recently, Mumford (1953) records finding a skull in Hamer Cave, Mitchell, Indiana. Thus it is apparent that although the red bat does occur in caves, occurrences are erratic and do not favor explanation, since the circumstances involved are poorly known.

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W. B. QUAY AND JEROME S. MILLER, *Division of Mammals, Museum of Zoology, University of Michigan, Ann Arbor.* *Received September 11, 1954.*

RECORD OF A FEMALE HOARY BAT, *LASIURUS CINEREUS*, AND YOUNG IN SYRACUSE, NEW YORK

On July 1, 1953, the writer received a freshly killed female hoary bat with two well-grown young. The young bats were attached to the mother's nipples when captured and it is believed that she was flying with them. Table 1 presents weights and measurements for the mother and young.

The young bats had their eyes open and were very well developed. Although the basic pattern for the marking of the adult was evident, the young differed decidedly in coloration from the mother. Their hair was much shorter and thinner and a uniform silvery gray on the back. The posterior half of the wing membranes was black. The anterior half was flesh-colored except for black patches over the elbows. The head and neck lacked the black ruff that is so noticeable in the adult. The sides of the head were somewhat tawny; the muzzle, ears, thumbs and feet black.

TABLE 1.—*Measurements in grams and millimeters of hoary bat and young*

	Weight	Length	Tail	Foot	Ear	Tibia	Longest finger	Thumb	Wing spread
Mother.....	26.6	139.0	58.0	10.0	20	22.0	104.0	11	368
Young male ..	12.3	98.5	41.5	9.0	12	16.5	58.5	10	203
Young female	11.8	93.6	41.5	9.5	12	16.5	58.5	10	203

The combined weight of the young was 24.1 grams or 90.6 per cent of the weight of the mother. If the mother was carrying the young in flight she was burdened by a weight nearly equal to her own.

The bats were killed not far from a mixed hardwood forest and within 150 feet of a mixed pine plantation.—LEROY C. STEGEMAN, *College of Forestry, State University of New York, Syracuse. Received September 17, 1954.*

A NEW NORTHERNMOST RECORD OF THE YELLOW BAT, *DASYPTERUS FLORIDANUS*

A yellow bat, *Dasypterus floridanus* Miller, was captured by Mrs. St. Julien R. Marshall in the front yard of her home at 1216 Little Bay Avenue, Willoughby Beach, Norfolk County, Virginia on May 8, 1954. A search of the literature reveals that this species has not been observed previously north of Charleston, South Carolina (Coleman, R. H., Jour. Mamm., 29: 293, 1948).

The bat was first noticed by four year old Barbara Michael Cheshire, who was accompanying Mrs. Marshall on a nature study trip. The animal was hanging without concealment four feet above the ground from several small twigs on a leafy lower branch of a Lombardy poplar. Although the day was clear and sunny with a strong breeze, the bat was in a state of lethargy when discovered shortly after noon. Three hours later it was still in this state, but became quite active after five minutes of warming in the hands of the author. When released in a room it flew about gracefully and without sign of injury. It was kept in a cage for observation, but remained lethargic most of the time, usually hanging suspended from the fork of a twig in the cage. In this position it kept its tail and interfemoral membrane curled back over the fork of the twig. It was most gentle, and showed no aggressive behavior or disposition to bite. It appeared to like to be handled, a phenomenon I have observed in other captive bats. Perhaps it enjoyed the warmth of my hands. It was fed a mixture of cottage cheese and ripe banana, with vitamin B_{12} added, a ration that I have found to be suitable for other bats, particularly the big-brown bat, *Eptesicus*. Although the yellow bat ate well, it gradually lost strength and died after six days in captivity.

The following measurements were taken in the flesh: Total length, 131 mm.; tail vertebrae, 57; hind foot, 12; forearm, 52; wing spread, 375 mm. A post mortem dissection of the animal revealed three embryos, each of which measured 12 mm. in total length. The specimen was prepared as a study skin and was deposited in the Norfolk Museum of Arts and Sciences as a gift from Mrs. Marshall. The specimen has been examined and its identification confirmed by C. O. Handley, Jr., of the U. S. National Musuem.

The capture of a pregnant yellow bat so far north of its known range presents a perplexing problem. The place of capture is a rather heavily populated residential beach, with sparsely distributed trees. The bat was found unconcealed in full sunlight. The rather cool weather of May 8 and several previous days may account for the peculiar circumstances of its discovery, but not for its occurrence so far north of its known range.—R. H. RAGEOT, *Norfolk Museum of Arts and Sciences, Norfolk 10, Virginia. Received October 24, 1954.*

ECTOPARASITES FROM SOME SPECIES OF BATS FROM WESTERN NORTH AMERICA

The ectoparasitic fauna of many species of bats has only begun to be known. A summary catalogue for the Chiroptera prepared by Stiles and Noland (Bul. Nat. Inst. of Health, 155: 603–742, 1931) presents a list of bats and their known parasites complete to the year 1930. G. M. Allen (BATS, Harvard Univ. Press, 1939) reviewed much of the literature concerning parasites of bats and presented an excellent synthesis of this data. More recent data are to be found in monographs on various groups of arthropods (such as ticks, mites, fleas and flies) and in descriptions of new bat-inhabiting species. Accounts of a faunistic nature are poorly represented in the literature; therefore it is thought that the following notes, although admittedly incomplete, will indicate something of the ectoparasitic fauna for the 12 kinds of western North American bats considered.

I wish to acknowledge the assistance of Dr. Furman of the Department of Entomology, University of California, Berkeley, who most kindly identified the parasites. The specimens reported upon were obtained at various localities in San Diego County, California in the months June, July, August, and September, 1946. The author was aided in their collection by Dr. Keith L. Dixon of Texas Agricultural and Mechanical College.

It seems likely that most, and perhaps all, species of bats have ectoparasites of one sort or another. Certainly some individuals of all species that we collected were infested. Observations indicate that bats that were in colonial gatherings were more often parasitized than were bats that roosted alone. Nursery colonies (adult females with young) that inhabited warm places (e.g., barns, attics) had a higher incidence of parasites than did nursery colonies that roosted in cooler places (caves, tunnels, and rock crevices). The extent of individual infestation varied but on no occasion was an animal obtained that appeared in ill health because of the ectoparasites it carried. Most of the parasitized individuals harbored two or more species of parasites, and often particular species were restricted to a specific area of the host's body. For example, one kind might be confined to the membranes and another to the furred parts. We found mites, ticks, fleas, flies, and bugs infesting the bats studied.

LIST OF HOST SPECIES AND PARASITES

Choeronycteris mexicana.—Mr. A. C. Olson removed the ectoparasites from several bats of this species. There were seven mites, *Spinturnix* and two unidentified streblid flies.

Myotis yumanensis sociabilis.—Bats of this species obtained from a large colony roosting in an inspection tunnel of the Hodges Dam were found to be infested with mites of the genus *Spinturnix* and fleas of the genus *Myodopsylla*. Infestations as high as ten mites and three fleas were recorded for some bats. The mites were on the membranes and the fleas in the body fur. Other *sociabilis* procured from the attic of a winery at Escondido harbored fleas of the genus *Myodopsylla*. A single *sociabilis* taken from a large group ensconced above the ceiling in a barn near lower Otay Dam had five mites (*Spinturnix*) and one flea (*Myodopsylla gentilis*).

Myotis thysanodes thysanodes.—Twelve bats of this species, taken from a deserted mine tunnel 4.8 miles east of Laguna Junction, harbored mites of the genera *Spinturnix* and *Ichoronyssus* and numerous nycteribiids (unidentified).

Myotis californicus californicus.—Bats of this species obtained from a small nursery colony in a barn at Hulbards Grove were found to be infested with mites of the genus *Ichoronyssus*. The mites were confined to the membranes and averaged three per host. Dr. Furman noted that these mites were identical with those obtained from two other bats (*Corynorhinus r. pallescens* and *Myotis t. thysanodes*).

Myotis californicus stephensi.—Five mites of the genus *Spinturnix* were collected from a single *stephensi*, and several other individuals were found with one to two of these mites. The mites were confined to the wing membranes. One bat had a larval tick (unidentified) attached in the skin of the abdomen.

Myotis subulatus melanorhinus.—Several nymphal mites of the subfamily *Liponyssinae* were taken from a bat of this species that was obtained from a corridor in the biology building at San Diego State College. Other bats of this species taken singly from various deserted mine tunnels near San Diego were free of ectoparasites.

Pipistrellus hesperus merriami.—Only two individuals of the 30 or 40 bats of this species that were examined had ectoparasites. One bat had several mites of the genus *Steatonyssus* on its membranes and a single larval tick *Dermacentor* attached to the skin of the abdomen; the other individual had a bedbug *Cimex* on the upper surface of each radius. All of the pipistrelles were obtained as they came to drink at Agua Caliente Spring. *P. hesperus* is usually a solitary species, roosting singly, often in rock crevices.

Eptesicus fuscus pallidus.—Ectoparasites were obtained from many individuals that were taken from colonies. Mites of the genus *Spinturnix* were removed from the membranes and frequently as many as eight or ten mites were collected from a single bat. Several bedbugs (*Cimex*) were found; these were always attached to the dorsal surface of the radius and two or three per bat was not uncommon. Each of several solitary roosting *Eptesicus* that we encountered was without ectoparasites.

Corynorhinus rafinesquii pallescens.—This bat was found to harbor several kinds of ectoparasites. Many of the bats examined were heavily parasitized and yielded eight or nine mites of the genus *Ichoronyssus*; three or four streblids (unidentified) and two or three nycteribiids (unidentified). The mites seemed to be confined to the membranes, but the two dipterans were found equally often on furred or membraneous areas although presumably they prefer the furred parts.

Antrozous pallidus pacificus.—Several nursery colonies of these large bats were visited and many ectoparasites were collected. Three genera of mites (*Spinturnix*, *Steatonyssus* and *Whartonia perplexa*), a larval tick (*Dermacentor*) and a nycteribiid (unidentified) comprised the fauna. The mites, as usual, were confined to the membranes, the flies chiefly to the furred parts and the ticks attached to the skin of the ventral surfaces. Infestations as high as 20 mites, five or six wingless flies, and three or four ticks were common. It is of particular interest to note the presence of ticks on these ground-feeding and low-foraging animals. It is easy to picture them in their low flight brushing against a peripheral branch, and in such a manner conceivably the ticks might have been acquired.

Tadarida mexicana.—Although many colonies of these bats were visited, collections of ectoparasites were not attempted in most instances. The following notes are hardly indicative of the degree of infestation nor of the ectoparasitic fauna of *Tadarida mexicana*. Field notes often mention the numerous ectoparasites seen but few were saved. The single collection made, was taken from bats that were found beneath a bridge two miles east of San Pasqual. Numerous nymphal mites of the subfamily Liponyssinae and several fleas (possibly *Myodopsylla*) were obtained.

Eumops perotis californicus.—Two of these rare molossids were collected from a rock crevice one and a half miles north of Barrett Junction. One of the bats yielded several polyctenids (*Hesperoctenes eumops*).—Philip H. Krutzsch, *School of Medicine, 300 Pennsylvania Hall, University of Pittsburgh, Pittsburgh 13, Pennsylvania.* *Received September 24, 1954.*

FREE-TAILED BATS, AND MELANISTIC MICE IN OREGON

Kenneth E. Stager (Jour. Mamm., 26: 196, 1945) reviewed the history of *Tadarida mexicana* so far as it was known in Oregon up to that time. In addition to the specimen taken by Dennis Constantine at Medford, Oregon on October 1, 1940, now number 2846 in the Jewett collection, three others of this species taken by Wayne W. Wells were sent me in the flesh. They were taken by Mr. Wells from a "large colony" living in a building in Ashland, Jackson County, Oregon, on February 6, 1954.

Last winter some school boys captured several live black mice that were living in some stored hay. Some of these were kept alive for some time as pets at the local school in Joseph, Wallowa County, Oregon. On May 4, 1954, Miss Ruth DuBois, a local school teacher who is

much interested in natural history, sent me an adult female and a half-grown young for specimens. These proved to be *Microtus montanus*, a locally abundant species.

Of the several hundreds of *Microtus* of various species I have trapped during the past 50 years in the northwestern states, these are the first melanistic specimens I have ever seen or heard of in this region.—STANLEY G. JEWETT, *Portland, Oregon. Received October 21, 1954.*

TRANS-UTERINE MIGRATION OF BLASTOCYSTS IN THE EASTERN SKUNK

Trans-uterine migration of blastocysts occurs in several kinds of fur animals having a bicornuate uterus. This has been demonstrated in the raccoon (Llewellyn and Enders, Jour. Mamm., 35: 439, 1954) and in the mink (Enders, Proc. Am. Philosophical Soc., 96: 692-755, 1952). No evidence of this phenomenon was found in the seal (Enders, Pearson, and Pearson, Anat. Rec., 94: 213-228, 1946). This note establishes the occurrence of trans-uterine migration of blastocysts in the eastern skunk (*Mephitis mephitis nigra*).

Evidence of blastocyst migration in skunks was obtained following unilateral ovariectomies performed on five skunks in 1953. The operation consisted of removing one ovary completely along with the ovarian capsule, oviduct, and proximal end of the uterine horn. The severed end of the uterus was closed with a suture. Only one of the above skunks was successfully bred and a later operation on it revealed one embryo in the right horn of the uterus and another in the left. This animal, one of a litter born in captivity on June 13, 1952, was intentionally isolated from contact with any males in 1953, and was bred for the first time in 1954. The above indicated migration of blastocysts does not always take place in the skunk. Records are available of two or three embryos in one horn and none in the other.—LEONARD M. LLEWELLYN AND ROBERT K. ENDERS, *U. S. Fish and Wildlife Service, Laurel, Maryland and Swarthmore College, Swarthmore, Pennsylvania. Received September 17, 1954.*

BLACK BEAR DENNING IN TREE

Black bears (*Ursus americanus*) in the northern part of their range normally go through a long period of winter dormancy, usually denning in a hollow log, cave, or even a sheltered depression in the ground. During the winter of 1953-54 an unusual instance of a bear denning in a live, standing tree at some distance above ground was reported in northern Michigan. The following information was given me by District Game Supervisor Otto DeWaard of Newberry.

Woodsmen working in late March near Blaney Park in the southeastern part of the Upper Peninsula were surprised when felling a large pine tree to see a bear scurry from an opening in the tree, walk across a log on a creek, and disappear into the brush. The animal was tracked and was found to have resumed its nap in a protected location about 150 yards away. The fallen tree measured 38 inches in diameter at the stump and 35 inches at the opening. The opening was at least 53 feet above ground with the floor of the den somewhat below this height. The den was filled with chips and other debris and despite its lofty situation must have provided fair shelter. The tree was located in a mixed conifer swamp containing cedar, spruce, and a few white pines. The bear was estimated to have weighed about 150 pounds, and was evidently a male or non-breeding female as no cubs were found.

There seemed to be little possibility that this was not a true winter den and that the animal had entered the hollow in the tree after leaving a ground den, since bears do not ordinarily come out of their dormant state in this part of Michigan until mid-April or later.

Jack Cameron, woods superintendent in charge of the logging operation, remarked that in his 36 years of work in the north woods he had never observed a similar instance of bears denning in this manner. To my knowledge such an account has not previously appeared in the literature.—D. F. SWITZENBERG, *Michigan Department of Conservation, Shingleton, Michigan. Received September 30, 1954.*

COLOR CHANGE IN THE BLACK BEAR, *URSUS AMERICANUS*

Mr. William J. Sheffler of Los Angeles, California gave me an account of his experience with a cub bear that appears to me to warrant placing on record. Mr. Sheffler is a naturalist with a lifelong interest in animals and much experience in field collecting of birds and mammals of western United States and Mexico. His private collection numbers some 4,000 well preserved and catalogued specimens. I have no hesitation in crediting his observations at face value.

In the spring of 1921, while in the Mogollon Mountains of New Mexico, he came upon a party of cattle men who had just killed a mother bear and one of her two cubs. The other cub, a female, was obtained by Mr. Sheffler and raised as a pet at his home (then in Texas).

The mother bear was a cinnamon color-phase animal. The cubs were fuzzy youngsters but the dead one was of darker shade than the one that was rescued. This latter animal developed into a true cinnamon-phase bear—a most enjoyable pet. After two years in captivity, however, it molted into a black-phase pelage. The animal was ultimately destroyed because of neighborhood problems involved, and the skin was preserved as a rug. I examined this skin in September of 1954 after a considerable amount of fading and abrasion had taken place.

Spread out in clear mid-day sunlight, the rug is seen to be of an extremely dark brown color shading to dull black on the legs. In the field or in reduced light of indoors such an animal would be designated a "black bear." The degree of "fading" that has taken place during 33 years of somewhat rough usage as a rug is hard to determine but was the subject of marked comment by both Mr. and Mrs. Sheffler as we examined it together. But both likewise emphasized the marked change that had taken place in their cinnamon bear pet at the age of approximately two and one half years. Is this a normal procedure or was it due to its artificial environment?—Loye Miller, *Museum of Vertebrate Zoology, Berkeley, California.* *Received September 25, 1954.*

FOOD CONSUMPTION OF HOUSE MICE AT LOW TEMPERATURES

It is a well recognized fact that under conditions of lowered environmental temperatures, the food consumption of isolated active mammals shows a definite increase (Campbell, 1945; Howard, 1951; Sealander, 1952*a*). The increased food intake is evidently necessary to supply more fuel for increased metabolism and consequently more production of body heat to maintain normal body temperature. An abundant supply of food in live-trapping small mammals in winter has also been shown to be an important factor in their survival (Llewellyn, 1950).

However, in gregarious animals there is often another factor quite important in the maintenance of body heat in cold weather. This is the huddling effect of numbers of animals together. The value of this factor in survival of small mammals has been shown by several workers (Howard, 1951; Sealander, 1952*b*). The data presented here further indicate that huddling together and sharing of body warmth may be an important factor in body temperature maintenance in cold weather.

The study was conducted at Madison, Wisconsin, during 1949–50 in a vacated, unheated army barrack-building. Two large enclosures were made by lining the lower walls of two rooms with galvanized iron. Each room had a floor area of about 500 square feet. In each pen were placed four locations of food and water, and five units of cover. Wild adult house mice (*Mus musculus*) were then introduced. The main purpose of the project was to determine the effect of limited food supply on population growth, and a report on this aspect of the study has been published (Strecker and Emlen, 1953). The work was conducted under the supervision and guidance of John T. Emlen, Jr.

A weighed amount of food, consisting of a finely ground mixture of grains and meat scraps, was supplied for each twenty-four hour period. Fresh food was furnished each day, and the remainder from the previous day was collected for weighing. Thus total daily food consumption was determined. A maximum-minimum thermometer was used to record

daily temperature extremes. When the data on food consumption and on temperature extremes were compared, it was very apparent that there was a positive correlation during the colder months. That is, as temperatures lowered, the food consumption tended to decrease also. This is shown very clearly in the data from January and February, 1950 (Fig. 1).

During this time the temperature varied from about 0°F. to 42°F. The temperature data are, of course, only maxima and minima, so that they do not give an entirely accurate picture for any one day, since they give no indication of the amount of the twenty-four hour period that was in the upper or lower temperature range. There was also some change in the number of mice during this period, so the gradual trends in the food consumption have little significance. In the colony labeled Pen B, the number of mice from January 1 to the end of February declined from 78 to 72. In the colony labeled Pen C the number of mice changed from 31 to 24.

Statistical tests of correlation between food consumption and temperature extremes were made. The food consumption data were compiled by taking the deviation of any one day's total consumption from the average for that weekly period. This would tend to reduce any effect due to changing numbers or size of mice. Based on 56 samples the food consumption of Pen B showed correlation coefficients of .72 with maximum daily temperature and .50 with minimum daily temperature. Pen C showed correlation coefficients of .61 with maximum daily temperature and .50 with minimum daily temperature. All of these values are well above the 1 per cent level of significance.

Despite the crudity of some of the measurements, the relationship of the two factors appears to be very definite. The correlation is somewhat better with the maximum daily temperatures than with the minimum daily temperatures.

The food mixture was located in bowls at least five feet from the nearest shelter. All feeding was done at the bowls, since the mice could not carry off and store the finely ground material. When not feeding they stayed in the shelter units or wandered around the room. The rooms were quite isolated and undisturbed, so the mice came out readily to feed or move about in the daytime. In the shelter units they tended to congregate together in a

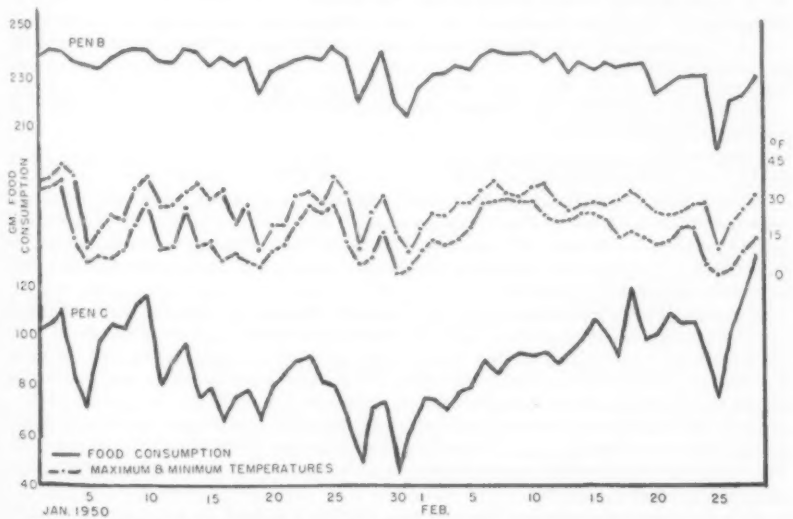

FIG. 1.—Graphs showing the daily food consumption in Pens B and C compared to maximum and minimum daily temperatures.

small area, rather than utilizing all the shelters. During the winter all the mice in the colony were often found in only two or three of the five possible shelters, and were in only a small area within the shelter. Attempts were made to measure the temperature inside the shelters containing mice. Such measurements were rather crude, but did indicate that the "inside shelter" temperature was considerably higher than the outside room temperature, with readings as high as 60°F.

By waiting quietly, one could easily observe the mice feeding. In cold weather they would dash out to a food bowl, eat for a few moments, and then run quickly back to the shelter, with no tendency to wander around, as they often did in warm weather. The decline in food consumption associated with decreasing environmental temperature probably meant that the individual mouse ate slightly less. All evidently ate sufficient amounts of food, since weight and general health were well maintained during this period. However, when it was very cold in the room, evidently the impetus to get back to the warmth of the group caused a decrease in the amount of time spent feeding. The high correlation with maximum daily temperature would be expected, for although the maximum temperature usually came during the daytime, the mice fed readily then because of the quiet, undisturbed conditions.

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ROBERT L. STRECKER, *Department of Zoology, Miami University, Oxford, Ohio.* *Received November 14, 1954.*

JANUARY BREEDING OF *PEROMYSCUS* IN NORTH CENTRAL COLORADO

Warren (THE MAMMALS OF COLORADO, 1942) reported the breeding season of *Peromyscus maniculatus* in Colorado as "spring and summer" with occasional records in April and late September. Beidleman (Jour. Mamm., 35: 118, 1954) recorded October, 1952, breeding in Colorado *Peromyscus* as evidenced by one pregnant and nine lactating females, and two males with descended testes.

Fourteen *Peromyscus maniculatus* were trapped January 2, 1954, in the foothills of northern Larimer County, Colorado at an elevation of 5700 feet. Two of the six females were pregnant; one contained five embryos five mm. crown-rump length and the other had six embryos of one mm. each. The testes of two males were scrotal in position. Testes length of all eight males varied from six to 11.0 mm.

Beidleman (*ibid.*) and Brown (Ecology, 26: 308–309, 1945) associated late breeding with above-average temperatures and subnormal precipitation. Manville (Jour. Mamm., 33: 389, 1952) felt no correlation existed between October breeding in Michigan *Peromyscus* and local weather conditions.

It is of interest to note that the January breeding followed an extremely dry fall in northern Colorado. The precipitation for the last four months of 1953 was only slightly more than one half the normal amount for the period. The mean average temperature

was 2.5°F. above the normal mean.—Edward B. Reed, *Zoology Department, Colorado A & M College, Fort Collins. Received September 30, 1954.*

VOCAL SOUND PRODUCED BY THE KANGAROO RAT, *DIPODOMYS SPECTABILIS*

The sounds produced by kangaroo rats have been sparingly mentioned in the literature. The principal noise seems to be a tapping or scratching by the hind feet. Vocal sounds are apparently rare, most reports of them being negative. Price (in Allen, Bul. Amer. Mus. Nat. Hist., 7, Art. 6: 193–258, 1895) describes a low chuckle in *Dipodomys spectabilis*. This observation has been corroborated by Vorhies and Taylor (U. S. Dept. Agric. Bul. 1091: 1–40, 1922) for *D. spectabilis* and by Tappe (Jour. Mamm., 22: 117–148, 1941) for *D. heermanni tularensis*, but these authors heard the sound only when the animals were disturbed. Vorhies and Taylor also state that *D. spectabilis* would "squeal much like a cornered house rat" when teased. Tappe describes a "plaintive, low pitched, rattling squeak" uttered by *D. heermanni* while struggling to be released from a person's grasp. Both Vorhies and Taylor and Tappe claim never to have heard a vocal sound produced by a free-living individual. Ketcham (Nat. Geog. Mag., 78: 537–548, 1940) describes various noises made by semi-tame, but free, *D. deserti* as angry squeals, purring growls, grunts, and cluckings, while young animals "cry like newborn puppies". Most of these seem closely to resemble the noises described by Vorhies and Taylor and Tappe.

During the summer of 1954 my wife and I casually collected mammals in the western United States. We became acquainted with *Dipodomys spectabilis* when we camped among a large aggregation of mounds a few miles east of Oracle Junction, Arizona, and set our traps in the area. Here we commonly heard a sound, almost surely vocal, which has not before been recorded for a kangaroo rat. At about one o'clock AM on July 12, I wakened to hear, at frequent intervals, a very high-pitched "peeee" lasting about a second. Having heard of the calls of grasshopper mice (*Onychomys*), I attributed the sounds to them. As I checked my traps, however, it became evident that these sounds were coming from the mounds of the kangaroo rats. That this was so was proved by an observation. As I approached a mound by the light of a Coleman lantern, I heard the high sound coming from this mound. An apparent answer was heard some distance away. As this exchange continued, a kangaroo rat emerged, seemingly unfrightened by my light, and answered its neighbor. When it had moved some distance off its mound, I tried to capture it. After this no further sounds were heard in the vicinity. The animal was caught and proved to be a well-grown immature male *Dipodomys spectabilis*, 287 mm. total length, weighing 77.0 gm.

Since we did not realize that these sounds had not been reported, no further pertinent observations were made, although we spent two hours watching the activities of this and other species of rodents. It seems doubtful that only the immature kangaroo rats make these sounds, for they were heard from all quarters of the area very commonly. The fact that Vorhies and Taylor never heard them seems almost incredible.

Several other species were present and active, including *Dipodomys merriami*, *Perognathus baileyi*, *Peromyscus eremicus*, *Peromyscus maniculatus sonoriensis*, and *Neotoma albigula*. None of these was associated with any sound.—Robert H. Gibbs, Jr., *Department of Conservation, Cornell University, Ithaca, New York. Received December 1, 1954.*

REMOVAL OF FOREIGN QUILLS BY PORCUPINES

Are porcupines (*Erethizon dorsatum*) immune to the effects of the quills from another, or do they too experience the discomforts that any other mammal does when quilled? Over a period of years, observations and experiences with the porcupine colony at the Vivarium of the University of Buffalo, have supplied information on this question.

The quill-studded club-like tail of a porcupine is very muscular, and with a strong direct blow it can drive several, to many very sharp quills as much as a half-inch or more into the body of its victim. When a quill has been buried in the victim's muscles, the movements of the muscles cause their fibers to catch against or engage the tips of the surface

scales on the quill, and the contraction of the muscle fibers in turn draws the quill further into the victim's body tissues. Such a migratory quill or quill fragment may travel at the rate of nearly an inch per day (Shadle, Jour. Mamm., 28: 180–181, 1947), (Shadle and Po-Chedley, Jour. Mamm., 30: 172–173, 1949).

The reactions of a mammal that has been quilled by a porcupine vary considerably according to several factors, some of which are: (a) the number of quills involved in the quilling, (b) the location of the area affected and the degree of sensitivity of the region involved, (c) the depth to which the quills penetrated the area, (d) the ability of the animal to endure pain and discomfort, (e) the excitability of the victim, (f) the length of time that the quills have been buried in the tissues, and whether or not infections have developed, (g) the amount of further penetration of the quills due to muscular activity, and other factors may also be involved.

The information on the effects and the reactions of humans to the quills are more readily obtained and are more complete because the human can describe his feelings and the subsequent results. From the author's considerable experience with quills in his own body, he is convinced that descriptions of the "horrible" effects of being quilled are often much exaggerated (Shadle, Amer. Nat., 89: 47–49, 1955).

Shallow penetration of the quills is often accompanied by an itching sensation. Captive porcupines are frequently observed scratching an area that has just been quilled, and they also rub the area against a post, beam, or other object, particularly when the face, mouth, or head have been involved. A fore paw may be used to grasp and pull out the foreign quills when within reach, and when not too deeply buried in the flesh. In removing foreign quills that can be reached with the mouth, the porcupine often uses the upper and lower incisor teeth like pincers and carefully seizing the quill, pulls it out, drops it, or removes it from its mouth with its tongue or with one of its fore feet. Occasionally pressure of the teeth on the spine may cut it into two pieces, leaving the point still buried in the flesh. However, the tooth pressure applied to the foreign quill is usually adequate to prevent the teeth from slipping off the quill, and strong enough to pull it out of the flesh.

When sufficiently aroused to attack or to fight, a porcupine will unhesitatingly seize another one at any point in the body, regardless of the number or size of the quills present in the area, and in so doing the attacker may get several of them in its mouth and face. At times these animals may be so much aroused and so excited, that they appear to be unaware of quill penetration until their excitement has subsided.

One of the finest demonstrations of numbers of foreign quills being removed by a porcupine occurred at the Vivarium when two three-year-old males, "Pinkie," an albino, and "Johnie," a normal colored animal, were having their cages exchanged. Although as young animals these two males had played and grown up together, as mature breeding animals they were unfriendly and could not occupy the same cage.

For some weeks, the albino had been less tractable than usual and had objected to being handled; he would become non-cooperative and would turn away and retreat every time he sensed that he was about to be picked up or touched. Since he weighed about 23 pounds, his attitude of non-cooperation often made handling awkward and difficult, particularly when he struggled to hang on to something. In making the exchange of cages, "Johnie" was carried into the albino's cage and placed on the floor so that he faced the front of the cage. At the back of the cage, the albino was up on the rest shelf which was approximately breast high, thus making it hard to lift him up. Seizing him by the tail, his hind legs were lifted free from the shelf, but with his fore feet he clung to the shelf, from which he had to be pulled loose. When his claws suddenly let go, his heavy body swung down in such a way that the posterior and the outer sides of his right fore leg struck forcibly against the partially erected, heavy quills of "Johnie's" lower back, thereby driving over fifty strong, sharp quills deeply into "Pinkie's" limb. To this painful experience, he reacted very promptly. He showed considerable agitation and as soon as he was set down in his new cage, he discharged a large amount of urine and immediately prepared to remove the foreign spines. He reared up, sat on his haunches, lifted the quilled

arm and taking one of the foreign quills between his upper and lower incisors, he pulled it out. The quills were so well buried in his flesh that it took a hard pull to dislodge them, but apparently none broke off in the process. When a spine was pulled out, he would take it from his mouth with his left fore paw and drop it to the floor. At times the left front paw would seize and hold on to the right limb while the spines were being pulled out by the incisors. In this manner he removed over twenty which were within reach of his mouth, but more than half of them still could not be reached because they were on the posterior side of, and directly behind the thick part of the right fore leg.

Although several attempts were made to assist him in the quill removal, he would not allow anyone to handle or even touch him. "Pinkie" then did a rather surprising thing which enabled him to remove more spines. Reaching across with his left fore paw and taking hold of the outside of his right fore limb, he pulled it towards the left which rotated the muscular portion so that the quills, which previously could not be reached, were thereby drawn within reach of his teeth. He repeated this act several times and managed to remove all but twelve of the foreign quills that were too far back, and too high up on the limb to seize with his incisors. Since he had become quite excited by this experience and still would not allow me to handle or help him, he was given an anaesthetic (ether) and the last spines were quickly taken out.

Observations of many captive porcupines quilled when fighting or when the males became too ardent in courting and testing non-cooperative females have furnished sample evidence that the porcupine experiences the same general discomforts that other animals feel when quilled. Scratching the affected area during the itching sensation, rubbing the region, which tends to relieve pain, the marked activity, and the nervous excitement evinced by the porcupine that has been well quilled parallel the effects experienced by a person, except that there was no vocalization or outcry on the part of the porcupines in any of the cases observed.—ALBERT R. SHADLE, *The Biology Department, University of Buffalo, Buffalo 14, New York.* *Received October 26, 1954.*

NUTRIA, *MYOCASTER COYPUS*, IN MINNESOTA

Nutria, large, semi-aquatic rodents, were brought from South America to the United States by fur farmers. Either through liberation or escape, wild populations have been established, notably in Louisiana. In Minnesota both specimens and reports of feral individuals were received between 1947 and 1949.

One specimen (No. 2456 in Minnesota Museum of Natural History) was killed on the highway near Faribault, Rice County in Minnesota in the fall of 1947. Three specimens (Numbers 2804, 2805, 2806) from Lake of the Woods County in December, 1949, may have their origin from two sources, one at Rainy River, Ontario, and the other from near Ray, Koochiching County, Minnesota. Nutria were liberated near Rainy River, Ontario, just across the border from Baudette, Lake-of-the-Woods County, Minnesota, in 1948. Nutria were also released along the Rat Root River, near Ray, Koochiching County, Minnesota, between 1941 and 1945. Mr. Vivien Marble, living near Ray, began raising nutria in 1939. The limited income from the fur coupled with wartime food restrictions finally forced him to dispose of them. Since these liberations there have been scattered observations of feral nutria in this area; Mr. Marble wrote that they tend to build mud dams of a sort. Some had lost a part of their tails from freezing.

There have been no recent records of nutria in the state, so in all probability none of these were able to perpetuate themselves.—HARVEY L. GUNDERSON, *Minnesota Museum of Natural History, Minneapolis 14.* *Received September 24, 1954.*

NEW RODENT RECORDS FOR CHILE AND FOR TWO CHILEAN PROVINCES

A decade ago, Osgood (Publs. Field Mus. Nat. Hist., Zool. Ser., 30: 9–10, 1943) stated that existing collections probably furnished a "nearly complete picture of the whole mammal fauna" of Chile. This statement has proven somewhat rash, for Mann (Biológica,

Santiago, 2: 25, 1945; Investigaciones Zoológicas Chilenas, Santiago, 2: 4–5, Dec. 1950) has reported the occurrence of eight additional species in the northernmost province, Tarapacá, alone. Between September 20 and November 11, 1952, Mary Koford and I collected, for the Museum of Vertebrate Zoology, three dozen specimens of small mammals from the highlands of northern Chile. Included among these are three species of cricetid mice not heretofore recorded from Chile, although known from either, or both, Perú and Bolivia. These species were taken as follows:

Akodon berlepschii Thomas.—Two (including MVZ 116770) were trapped at Caritaya, 75 miles southeast of Arica, Province of Tarapacá, elevation 12,000 feet, alongside boulders on dry slopes.

Hesperomys lepidus ducilla (Thomas).—One (MVZ 116789) was trapped at Ojos San Pedro, 55 miles northeast of Calama, Province of Antofagasta, elevation 12,500 feet, in dry bunchgrass alongside a stream.

Phyllotis sublimis Thomas.—Eight (including MVZ 116793) were trapped at Toconce, 60 miles east northeast of Calama, Province of Antofagasta, elevation 14,000 feet, during a period of three weeks. These mice were common on dry sandy slopes near boulders and tufts of fescue (*Festuca dolicophylla* and others).

Two additional species of rodents were found in Chilean provinces from which they have not previously been reported. The hystricomorph chinchilla rat (*Abrocoma cinerea* Thomas) has been recorded by Mann from Tarapacá. We captured four (including MVZ 116801) at Toconce, Province of Antofagasta, about 200 miles south of the previous Chilean locality of record. These rats were caught in No. 0 steel traps placed in their trackways or at the mouths of their open burrows (two inches in diameter) at the bases of boulders or low resinous "tola" shrubs. On dry sandy slopes between low bushes and tufts of fescue, the round footprints, usually placed alternately as if the animal most often moved by running rather than by hopping, were followed for distances as great as 200 yards. Three captives, little injured by trapping, vigorously ate the three most common species of tola (*Lepidophyllum rigidum*, *Lepidophyllum quadrangulare*, and *Baccharis microphylla*), preferring the flowers and tips of branches.

On a subsequent trip, in August, 1953, I trapped a mole mouse (*Notiomys megalonyx* Waterhouse) at Fray Jorge, Province of Coquimbo, elevation 1000 feet, among shrubs and cactus at the foot of a long steep slope. This specimen (MVZ 118657) was taken about 150 miles north of the northernmost locality for the species (and genus) cited by Osgood (*op. cit.*: 157).—Carl B. Koford, *Museum of Vertebrate Zoology, University of California, Berkeley. Received September 25, 1954.*

BOTTLE-NOSED DOLPHINS SUPPORT REMAINS OF YOUNG

About 10:00 AM on August 4, 1954, while on a boat patrol in the Everglades National Park in south Florida, district rangers Vincent M. Mrazek and Lyle H. McDowell were passing through the middle of Whitewater Bay near Long Point (lat. 25° 17′, long. 80° 59′). Seeing two bottle-nosed dolphins (*Tursiops truncatus*) associating in the calm water with a small, whitish, floating object, the rangers circled back to investigate. The dolphins, one of which had been rather continuously bumping the object along with its snout, submerged and disappeared as the boat approached, but when the rangers came to within about 25 feet of the floating object, they discovered it to be the head of a baby dolphin. Its body had been cut away from the head very smoothly, suggesting the bite of a large shark. Having identified the object of the attention of the dolphins, the rangers withdrew 70 or 80 feet and watched for several minutes. The two apparently adult dolphins returned to the floating baby's head and remained close, often rolling within inches of it and sometimes bumping it gently with their snouts. The baby had probably been dead for some time, for the skin of its head appeared to be nearly white in color. Whitewater Bay is a roughly rectangular bay measuring about ten by five statute miles and strewn with perhaps seven or eight square miles of mangrove islands. It is consistently four or five feet deep, with a maximum of six, and is salty, being connected with the Gulf of Mexico five

miles to the west by a labyrinth of deeper channels. Bottle-nosed dolphins are often seen in Whitewater Bay, probably with greater frequency in the summer.

The writer (Moore, Amer. Midl. Nat., 49: 117–158, 1953) has reported in detail an observation in Everglades National Park waters of a single bottle-nosed dolphin supporting on its head a dead young one which had been bitten nearly in half just behind the dorsal fin, apparently by a large shark or barracuda. Since this young one measured only three feet four inches, and its teeth were still covered by the gums, it was thought to have died newborn or no more than a week or two old. It was estimated to have been dead three days, but while under observation it was being continuously supported on the head of the adult, who left it only momentarily at intervals to breathe.

More recently Hubbs (Jour. Mamm., 34: 498, 1953) reported an instance of a bottle-nosed dolphin of the California coastal waters (*Tursiops gillii*), swimming along in a school of four or five, supporting the dead body of a baby dolphin on its back against the dorsal fin. That one dolphin supported a dead young on its head whereas another supported its dead young one on its back against the dorsal fin may have been a difference of how the animal could accomplish its end in completely calm water as compared to water where there was some wave action. McBride and Hebb (Jour. Comp. and Physiol. Psychol., 41: 111–123, 1948) reported one instance of a captive mother bottle-nosed dolphin at Marine Studios raising its stillborn baby to the surface of the water as if to help it to breathe, and one instance of a mother whose older baby had died in the night, discovered the next morning holding her baby to the surface of the water. Writing of a total of five stillbirths and three successful births of bottle-nosed dolphins at Marine Studios, Kritzler (McBride and Kritzler, Jour. Mamm., 32: 251–266, 1951), mentions the efforts of the mother in "several" of the stillbirth cases to raise the dead young to the surface of the water. The observations at Marine Studios suggest the existence of an instinct of the mother *Tursiops*, when its infant offspring becomes helpless, to raise it to the air, and to support it there. Survival value of such an instinct is obvious. The three field observations reveal that this behavior does occur among free wild *Tursiops* in both the Atlantic and Pacific, and that it may be sustained in some instances until the young one has been dead for several days, or even reduced to nothing but the head. It seems reasonable to suppose that a dolphin could not accomplish this act of supporting its young at the surface in any considerable wave action. One wonders if this behavior might occur among other delphinid inhabitants of protected waters, but not among pelagic forms.—Joseph Curtis Moore, *Everglades National Park, Homestead, Florida.* *Received October 8, 1954.*

NOTES ON THE SPOTTED DOLPHIN, *STENELLA PLAGIODON*, AND THE FIRST RECORD OF THE COMMON DOLPHIN, *DELPHINUS DELPHIS*, IN THE GULF OF MEXICO

Through the courtesy of Mr. Stewart Springer, I had the opportunity to make Cruise No. 23 of the United States Fish and Wildlife Service M/V *Oregon* to the Western Gulf of Mexico during May and part of June, 1954, and to record the observations on the spotted dolphin, *Stenella plagiodon*, noted below. Sight records are summarized in Table 1 and Figure 1. The numbers in parentheses refer to Figure 1.

All of the observations of the spotted dolphin recorded in Table 1 were made in the immediate vicinity of the vessel, primarily around and in front of the bow, though on two occasions, positions (6) and (8), the individuals were seen to follow a large otter trawl to the surface as it was being hauled in. Both of these times the dolphins milled around the filled cod end of the net until it was actually brought on board. Only once, the afternoon record at position (2), did the animals stay with the vessel more than a few minutes, ten or less. They usually ran with the ship just at the bow, occasionally darting away and returning before disappearing very rapidly, as they had appeared. The ones at the bow usually held their speed with that of the vessel, which ranged from a near standstill to approximately ten knots. Their frequency of blowing also seemed to be correlated with

TABLE 1.—*Observations of spotted dolphins made aboard the M/V Oregon from May 7 to June 5, 1954*

Date	Position of Oregon		Position in Figure 1	Depth in fathoms	Miles to nearest land	Number of individuals
	Lat. North	Long. West				
May						
7	28°19′	90°19′	(1)	40	67	3
8 (AM)	27°50′	92°00′	(2)	170–235	166	Several
8 (PM)	27°50′	92°00′	(2)	170–235	166	2–25
13	21°44′	91°05′	(3)	36	62	3
13	21°39′	90°59′	(4)	19.5	52	2
13	21°07′	91°33′	(5)	17.5	64	1
16	18°43′	93°30′	(6)	35	20	3
28	26°15′	95°30′	(7)	1000	100	30 (est.)
June						
3	26°10′	97°00′	(8)	11	10	3
3	26°10′	96°54′	(9)	18	16	3
3	26°10′	96°40′	(10)	29	31	10
5	27°20′	96°20′	(11)	85	53	2–12

the speed of the ship. When moving rapidly they blew every 5–10 seconds, and when nearly motionless (when the vessel was almost stopped) they blew only once every 60–120 seconds.

Sexual behavior.—The *Oregon* was moving very slowly, taking in a long-line, at position (2) at about 1400 hours when a school of some 20–25 spotted dolphins appeared around and some distance ahead of the bow. The weather was warm and sunny, and the water surface very calm. Several sizes were present in the school, including a small individual that followed very closely with a larger one. Its actions were similar to those of a *Tursiops truncatus* calf observed with its mother at Marine Studios, Marineland, Florida, and it was assumed that this too was a calf with its mother. It remained with the larger one at all times and followed just under or to the right of the latter's tail region. There was also a very large, heavily scarred, individual present, perhaps a male. This scarring may have been a result of encounters with other dolphins, or of feeding attacks on large squids. These and the other spotted dolphins recorded in this note, exclusive of supposed calves, seemed to average some seven to eight feet in length, the scarred one being perhaps nine feet. Most of the animals at position (2) were in groups of two to six, lying side by side and head to head at or just below the surface. All members of each group rose to blow at precisely the same moment. These small groups were barely moving, if at all. Others in the school were swimming about at a moderate speed, "rolling" to breathe as they did so. Occasionally two individuals would apparently attempt to copulate, one remaining just beneath the surface in a normal swimming position and the second turning belly up beneath and almost parallel, its head slightly to the right of the one in normal position, its tail thus projecting to the left of that of the uppermost individual. This action was accompanied by some splashing with the tail which partially obscured vision from the bridge of the ship.

Eventually the vessel came to a dark patch in the water which on closer examination proved to be the remains of a large squid (pieces of large tentacles were seen floating on the surface). Unfortunately, circumstances made it impossible to divert the vessel in order to recover these fragments for identification, and only a piece of the skin that floated near the boat was collected. The dolphins' excited behavior and repeated passes through the vicinity of the remains indicated that the squid had probably been killed and was being eaten by the school. The school remained with the vessel for about 15 minutes before disappearing. Approximately 15 minutes later about eight dolphins reappeared and stayed with

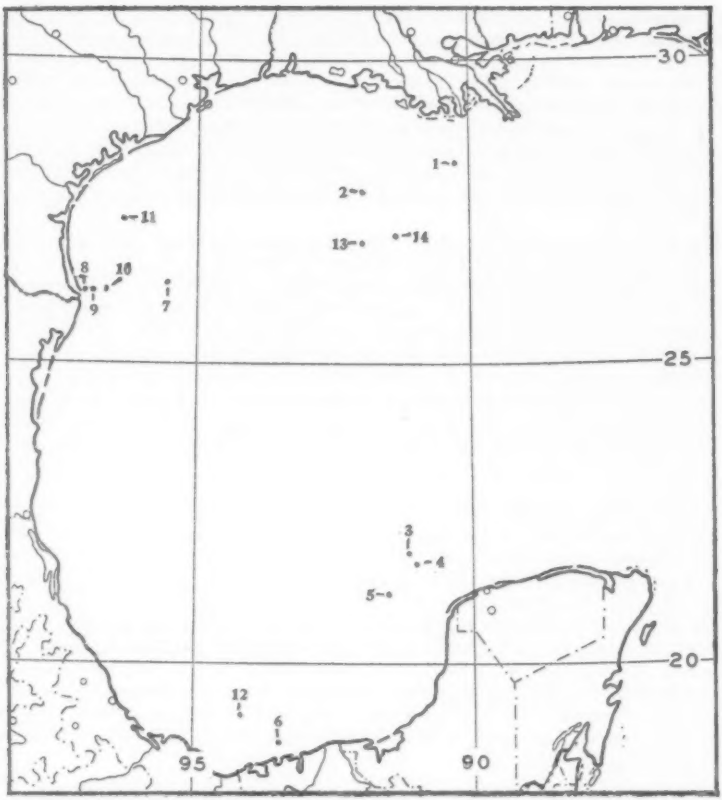

FIG. 1.—Approximate positions of the M/V *Oregon* in the Western Gulf of Mexico in May and June of 1954.

us for about 20 minutes until we got under way. There was little doubt that members of this second group were also attempting copulation, their positions and actions being the same as that described above. Occasionally one would vigorously slap the water several times with its flukes, and one jumped completely clear of the water in a low arc nearly parallel with the surface. These performances were repeated several times. One would also "stand on its tail" with its head completely out of the water facing the ship and remain so for approximately 15 seconds. I cannot say whether these were different schools or the same ones that disappeared and shortly returned.

Coloration of the young.—As noted above, there was at least one individual in the school at position (2) that was assumed to be a young calf. Several similar small individuals were observed at positions (7) and (11). Mr. Springer had pointed out early in the cruise that the young of this species did not seem to be spotted as are the adults. This is also reported by Kellogg (Natl. Geog. Mag., 77: 85 and Pl. XIX, 1940) who describes the calf as being a "uniform gray color." My first two observations of young did not afford the opportunity for careful note of this fact, though enough of the animal was seen each time to indicate that it was probably true. However, at position (11) several calves were present, one jump-

ing completely clear of the water several times. These were about half the size of the accompanying adults (which were obviously spotted). This brief moment in the air showed the calf to be a dark purplish-brown above, shading to a light gray-brown on the ventral side, rather than a uniform gray. There was no evidence of spotting, their color being very similar to the base color, without spots, of the adults. This different coloration of the young may be the basis for reports of mixed schools of dolphins offshore. Nichols (Jour. Mamm., 1: 87, 1920) for example reports a school of 35 Spotted Dolphins off North Carolina, one of which was "accompanied by a small gray porpoise swimming close beside it which looked like *Delphinus*." It seems quite likely that this small specimen was actually a spotted dolphin calf.

Also of interest are the following records of two other members of the family Delphinidae. The numbers in parentheses refer as before to Figure 1.

Short-finned blackfish, *Globicephala macrorhyncha*.—Approximately 30 individuals, tentatively identified as this species, were observed on May 17, while the vessel was stopped at position (12) over 700 fathoms, some 50 miles from the nearest land. The position was Lat. 19°05′ N., Long. 94°10′ W. The animals stayed at or just beneath the surface, apparently making no effort to do more than hold their position, and blowing at fairly long (20–30 seconds) intervals. They sometimes remained so singly, but were often seen in close groups of as many as nine, usually with all members heading in one direction. They were present for about 30 minutes, and showed no fear of the ship until it got under way and we attempted to harpoon one. They then avoided the vessel for a short time before disappearing.

Common dolphin, *Delphinus delphis*.—About 12 of this species appeared at the bow while the vessel was under way at position (13), Lat. 27°00′ N., Long. 92°00′ W., on June 13, over 600 fathoms some 148 miles from the nearest land. Several more were seen on the same day at position (14), Lat. 27°10′ N., Long. 91°22′ W., in some 750 fathoms approximately 120 miles from land. Gunter (U. S. Fish and Wildlife Service, Fish. Bull. 89: 550, 1954) states that this species is not recorded from the Gulf of Mexico, but that it may be expected there. He points out that the closest known record is that given by Moore (Amer. Midl. Nat., 49: 133, 1953) for a skull from Miami Beach, Florida. The records included here are thus apparently the first for this species from the Gulf of Mexico. I have a recognizable Kodachrome picture of one of these specimens taken as it rose to blow just beside the bow.—David K. Caldwell, *Department of Biology, University of Florida, Gainesville.* *Received October 22, 1954.*

AN ALTITUDINAL RECORD FOR BISON IN NORTHERN COLORADO

Several authors (Fryxell, Jour. Mamm., 7: 102–109, 1926; Warren, Jour. Mamm. 8: 60–61, 1927) have discussed the altitudinal range of the bison (*Bison bison*) in the Rocky Mountain West, giving records that confirm this animal's visitation in the above-timberline country of Wyoming and Colorado. Most of the records have been based upon location of skeletal remains. This present record is unique because it was included in the verbal report of an Arapaho Indian party, transcribed by Oliver W. Toll for the Colorado Mountain Club. A copy of this report is on file in the Naturalist Office of Rocky Mountain National Park, Colorado. These Indians were brought to the present location of the park in July of 1913 for the purpose of obtaining information on the area during its much earlier period of Indian occupation, prior to 1859.

According to their report, one winter about the middle of the last century a herd of buffalo cows climbed high onto the steeply ascending east slope of Thatch-top Mountain, one of the peaks on the continental divide in the present park area. Here the bison were caught by snow, and a band of Arapaho Indians, following on snowshoes, killed many of the beasts. This mountain, called "*haathaanon—tahou hut*" or "Buffalo Climb" by the Arapahos, rises to a height of 12,800 feet, the upper 1500 feet being above timberline and covered with an abundance of alpine vegetation upon which bison conceivably could have grazed. If the Indians' story can be believed, and Toll felt certain that it was true, this

account represents an unusually high ascent by bison at an unusual season of year.—Richard G. Beidleman, *Zoology Department, Colorado A & M College, Fort Collins. Received October 8, 1954.*

RELEASE, DISPERSAL, AND REPRODUCTION OF FALLOW DEER IN NEBRASKA

Because of the fine sporting qualities of the fallow deer, *Dama dama* Linnaeus, it has been introduced in many parts of the world. In the United States this deer has been released in several places, but little has been published as to the success of these introductions. It seems desirable therefore to note that fallow deer have been released in the state of Nebraska (Fig. 1).

The exact date of the release of the fallow deer in Nebraska is unknown; however, Mr. James H. Agar, Superintendent of the Lincoln, Nebraska, Park Department (*in litt.*, October, 1953) writes, "In the late 1930's, the City Park Department took approximately sixty white fallow deer to the Hall Ranch ten miles northwest of Petersburg, Nebraska". This point of release was in the middle of the Beaver River Valley, which is on the southeastern edge of the Nebraska sandhills in Boone County. In this valley there are extensive hay fields, good willow growths, and some corn fields. Dr. J. Henry Sather, Leader, Pittman-Robinson Surveys and Investigations for the State of Nebraska Game Forestation and Parks Commission, also reported (*in litt.*, June, 1954) that in 1946 he found fallow deer in Boone and Wheeler counties. He interviewed six residents in Wheeler County and one in Boone County. Excerpts from his record of these interviews made in July, 1946, are as follows: On or about June 25, P. Ballweg, T.23N-R.10W, section 20, Wheeler County, saw nine fallow deer in a hay meadow, and observed the first deer in his area four years ago. He said that he could approach on horseback to within ten yards of the deer. Robert Keinzain, T.23N-R.10W, section 21, observed twenty-one in 1945. H. C. Mignery, T.23N-R.10W, section 23, mentioned reproduction when he stated, "In 1944 the front feet of a fawn were cut off by a mower. I took the fawn back to the ranch and bandaged feet." Later, Mignery hit another fawn that had to be destroyed. Louis Demary, T.23N-R.10W, section 24, observed a fallow deer in 1936, and G. T. Titterington, T.23N-R.10W, section 22, saw one i-

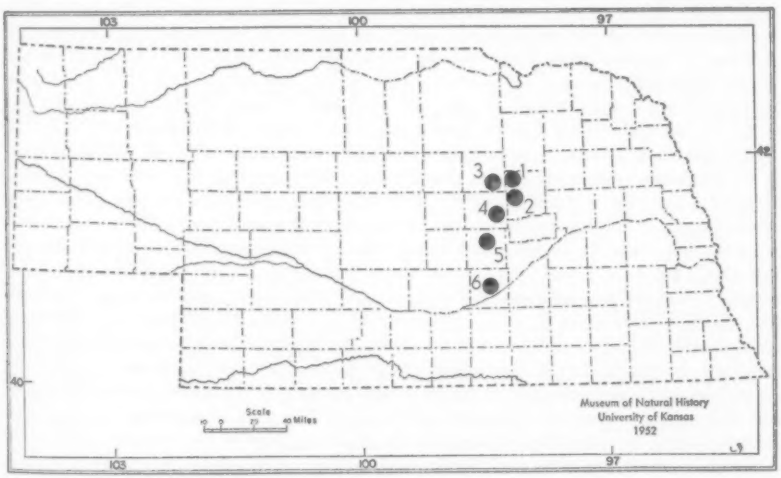

Fig. 1.—Locality records of fallow deer in Nebraska: 1. Where fallow deer were released. 2. Where fallow deer were observed to mate. 3. Where Sather obtained his information (also at point 1.). 4. and 5. Author's observations in 1954. 6. Agar's report of occurrence.

1939. Carl Klentz, T.23N-R.10W, section 25, observed a herd of twelve in 1946. F. A. Matson, T.22N-R.8W, section 23, Boone County, reported that the deer had ruined his orchard and that a herd of thirty stayed on the ranch the year round.

In July and August of 1954 I found fallow deer in Greely and Howard counties. Three individuals were observed on July 23 one and one-half miles east of Cotesfield along the Loup River, Howard County, and one was seen on August 8 along Cedar Creek, five miles northwest of Spalding, Greely County. Mr. Agar (*in litt.*, October, 1953) informed me that these have been observed in the area of Grand Island, Hall County, Nebraska.

Lydekker (THE DEER OF ALL LANDS: 130, 1898, London) and Whitehead (DEER AND THEIR MANAGEMENT: 164, 1950, London) recorded little of the breeding habits and behaviour of feral fallow deer, and Millais (THE MAMMALS OF GREAT BRITAIN AND IRELAND, vol. 3: 147, 1906, New York, London, and Bombay) made some mention of the breeding habits and behaviour of feral fallow deer in the Epping Forest. There is no account known to me of the actual mating procedure of this species in a feral or wild condition. Therefore, the following observations are noteworthy.

In the late afternoon (5:00 PM) of October 21, 1950, I observed a group of four male and two female fallow deer in a pasture approximately five miles south and two miles west of Petersburg, Boone County, Nebraska. This group seemed to be unusually excited although I was certain that they were not aware of my presence. Three bucks began to pursue one of the does down through a swale while the remaining buck and doe were seemingly not interested in the chase. The doe pursued by the bucks ran approximately one hundred yards straight away, halted abruptly, successfully dodged the bucks, and repeated her run. This behaviour was continued for ten minutes until the doe fell to the ground either in exhaustion or submission. The buck that arrived first in the immediate locality of the now resting doe had the largest antlers and seemed to be the oldest of the three males. He stood beside the doe, which was still lying on the ground, and then whirled about facing the two onrushing younger males, lowered his head, and stood motionless as the other two approached to within fifteen to twenty yards, and then moved toward the two bucks. This last movement caused one of the bucks to turn northward and leave the immediate area. The remaining male stopped, trotted diagonally away from the buck and doe and lay down about thirty yards away. The older buck, still beside the doe, then issued a series of deep-throated bellows unlike that of any of our native deer and resembling an extremely loud call of the bull frog except that the vibrations reaching the ear seemed fewer per second. This bellowing was continued intermittently, and several times the older buck approached the doe, touching her nose and ears with his nose. Each time the buck approached, the doe uttered a sound similar to that of a high pitched whine of a dog. The buck began circling the doe, now engaged in nipping small shoots of grass, and she seemed to be completely uninterested in the activity occurring about her. The older buck lowered his head at this time and charged in the direction of the remaining male, still about thirty yards distant. It stood motionless in the face of the charge until ten to fifteen yards separated the two; then the younger buck fled northward. The older buck returned to the doe and circled her more rapidly than before. Each circle brought the buck closer to the doe. Finally he stopped in such a position that she, still lying down, faced his rump. The buck then started a movement in which the posterior part of the flanks, hind legs, and their hooves were rotated in an up and down, then side to side "dance" while the front legs remained stationary. At the termination of this dance, the buck turned so as to face the doe, placed his nose at the side of her body and, pushing with his nose, forced the doe to rise. She ran some thirty yards and lay down again. The buck immediately followed and duplicated his dancelike ritual whereupon he caused the doe to rise and run again. This behavior occurred once more, but the fourth time the doe arose she remained stationary. Thereupon the buck mounted her and copulation took place. The position assumed during copulation was similar to that of domestic cattle, and the copulatory act was a continuous process lasting five minutes with only intermittent rests of a few seconds taken by the

buck. These rests were taken with the buck still mounted on the doe. After copulation the buck and doe remained together.

The entire sequence of events took thirty-two minutes and could be divided into five major stages: 1. Chase (10 minutes); 2. Aggressive movements among males (5 minutes); 3. Courtship plus aggressive movements among males (5 minutes); 4. Courtship immediately preceding copulation (5 to 7 minutes); and, 5. Copulation (5 minutes).

Fallow deer were released in Nebraska, have reproduced, are extending their range, and seem to have increased in numbers.—ROBERT L. PACKARD, *State Biological Survey, University of Kansas, Lawrence.* *Received September 6, 1954.*

MULE DEER MILK

An adult Rocky Mountain mule deer doe (*Odocoileus hemionius hemionius*) was shot about 6 AM, July 10, 1954. The doe, gross weight 132 lbs., 117 cm. crown-rump length, and estimated from her teeth wear according to the technic of Severinghaus (1949) to be about two years of age, was collected on Trisky Creek, National Bison Range. There was found upon autopsy only one large corpus luteum. The entire reproductive tract including the ovaries was preserved for further study in the laboratory. The fawn at her side was estimated to be 4-5 weeks of age.

A sample of milk was collected less than 15 minutes after she was shot by plunging a sterile needle into the main milk sinuses of the two hind quarters of the mammary gland. Approximately 50 cc. of milk was readily aspirated into two sterile vacuum tubes. The milk was placed in a refrigerator immediately upon return from the field, and was analyzed by the senior author next day. A second lactating doe was shot about 6:30 AM, August 16, 1954. The doe, gross weight 129 lbs., 115 cm. C-R length, estimated age two and one-half years, was collected on Pauline Creek, National Bison Range. A sample of milk was collected from her in a similar manner. A third lactating doe was shot about 6:30 AM, September 22, 1954, on Trisky Creek. The doe, gross weight 144 lbs., 132 cm. C-R, estimated age two and one-half years, yielded a milk sample for analysis. On September 9, 1954, Dr. P. L. Wright collected a sample of antelope milk from a female antelope shot on the Bison Range. His collection method was the same, namely by plunging a sterile needle into milk sinuses and aspirating a sample into a sterile syringe.

Table 1 gives the results of analyses of these milk samples.

This investigation was made possible through the cooperation of the Fish and Wildlife Service, The Montana Fish and Game Department, and the Montana Cooperative Wildlife Research Unit.

TABLE 1.—*Mammalian milk samples compared*

Species	Month	Sp. gr.	% total solids	% fat	% ash	Reference
Mule deer.....	July	1.044	20.78	8.13	1.66	Present report
Mule deer.....	Aug.	1.044	22.30	8.4	1.50	Present report
Mule deer.....	Sept.	1.040	27.63	13.6	1.39	Present report
Blacktail.....		1.046	20.4	8.3	1.44	Hagen '51
Antelope.....	Sept.	—	26.28	9.6	1.37	Present report
Sow.....		—	19.47	6.31	.99	Bowland, *et al.* '49
Reindeer.....		—	33.00	17.00	1.50	Heineman '19
Goat.....		1.030	13.12	4.07	.85	Heineman '19
Ewe.....		1.035	16.43	6.18	.93	Heineman '19
Mare.....		1.034	9.42	1.14	.36	Heineman '19
Cow.....		1.031	12.73	3.68	.72	Heineman '19

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LUDVIG G. BROWMAN AND HOWARD S. SEARS, *Department of Zoology, Montana State University, Missoula.* *Received September 1, 1954.*

ERYTHROCYTE VALUES, AND ALIMENTARY CANAL *p*H VALUES IN THE MULE DEER

Rocky Mountain mule deer (*Odocoileus hemionius hemionius*) on the National Bison Range, Moiese, Montana were shot at monthly intervals as part of another study. It was felt desirable to collect blood and *p*H data when possible from a wild ruminant in this refuge area. Very little is known about blood values, the *p*H of the gastro-intestinal tract, and other vital physiological data about our native big game. This investigation was made possible through the cooperation of the Fish and Wildlife Service, the Montana Fish and Game Department, and the Montana Cooperative Wildlife Research Unit.

The deer were hunted on the range, and care had to be taken to shoot only selected animals. When shot at long range animals bled themselves out. In rocky, hilly country more than 15 minutes may have elapsed between the shooting and our arrival at the carcass. Only those blood samples are included in this report that were collected less than 15 minutes after the animal was shot. Blood was aspirated from the jugular, or other large vein, into sterile, heparinized syringes, and injected into sterile vacuo-tubes. All blood samples were refrigerated immediately upon return from the field. All blood analyses were made in the laboratory on the day following the collection of the sample.

Specific gravity of the blood was determined gravimetrically at room temperature; hemoglobin determinations were made using a Sahli-Adams hemometer; erythrocyte and total white cells were made using a Levy corpuscle counting chamber; and packed red cells were determined by centrifugation of whole blood.

The animal was eviscerated promptly after bleeding and the intact digestive tract from the esophagus at the diaphragm to the anus was removed. Incisions were made at selected points along the alimentary canal, samples of their contents collected, and numbered tags were attached to the site. Fecal pellets from the colon and rectum were macerated to a soupy consistency in an equal volume of distilled water. All *p*H readings of the gastro-intestinal tract were made in the field as rapidly as possible, using a sample of approximately 25 cc. diluted with an equal volume of distilled water.

After all *p*H readings were made the gut was dissected out and measured, and *p*H readings and sample sites along the intestine were correlated. Care was taken not to stretch the freshly dissected alimentary tract for purposes of measurements in so far as field conditions permitted.

All *p*H readings were made with a portable Beckman *p*H Meter, Model M, checked periodically in the field against a standard buffer. All measurements of the freshly dissected tract were made in the field using a 50-foot steel tape laid out on the ground. Ages of all deer were based on the tooth development and tooth wear technic of Severinghaus (Jour. Wildlife Mgt., 13: 195, 1949).

Results.—Apparently the physiological condition of the deer is revealed to a considerable extent by the blood picture (Table 1). The hemoglobin content seems to be a better indication of general physical well being of the deer than does the red blood count. For example deer No. 59 impressed us in the field as being a sick animal at the time of autopsy

TABLE 1.—*Blood values in female mule deer from Western Montana*

Datum	Deer No.										
	31	33	34	38	45	48	53	59	61	65	Ave.
Date killed	12/12	12/16	12/16	12/22	2/13	3/13	4/11	6/11	6/11	8/16	
Hour killed	9 AM	11 AM	3 PM	1 PM	3 PM	8 AM	7 AM	11 AM	8 PM	6 PM	
Age in yrs.	6½	1½	1½	1½	2½	8–9	2½	1	6-7 da.	2½	
Gross body wt. in lbs.	117	97	106	102	129	99	122	72	75	129	
C—R length in cms.	130	116	110	126	123	126	123	99	54	115	
Sp. gr. of whole blood	1.041	—	1.044	1.044	1.054	1.054	—	—	1.044	1.048	1.047
Hemoglobin gms./100 ml.	12.1	13.0	14.1	10.2	—	15	16.5	9.5	11	14.0	12.8
Red cell count (millions/cu.mm.)	5.23	7.58	11.77	7.21	11.05	9.98	12.72	8.31	7.28	10.77	9.19
Total white cell count (thousands/cu.mm.)	5	3	1.8	3.8	3.3	3.2	2	(22)	(26)	3.5	3.3
Packed red cells % of total bl. vol.	38.2	36.8	42.7	32.1	45.7	42.4	42	—	34.7	41.9	39.6
Remarks on condition	Thin	Thin	Fair	Thin	Fair	Thin	Thin	Very poor (sick)	Held 9 hrs.	Fair (dia. of r.b.c.—5.7 micra)	

TABLE 2.—*Comparative blood values*

Species	Sp. gr.	Hemoglobin gm/100 ml.	Red cell count	White cell count	Packed cell vol. %	Reference
Goat	1.042	10.6	—	5+	34	Albritton, 1951*
Pig	1.046	13.3	6.9	7+	41.5	Albritton, 1951*
Ewe	1.051	12.6	11.6	4+	32	Albritton, 1951*
Cow	1.053	12.9	8.0	5+	38.6	Albritton, 1951*
Blacktail deer	—	(87.2%)	9.9	—	45.1	Rosen & Bischoff, 1952†
Calif. mule deer	—	(101.3%)	10.3	—	42.9	Rosen & Bischoff, 1952†
Rocky Mt. mule deer	1.047	12.8	9.2	3+	39.6	Present report

* Ed. HANDBOOK OF BIOLOGICAL DATA (Standard values in blood), A.I.B.S., Nat. Res. Council, U.S. Air Force, Dayton, Ohio. Tech. Rept. 6039: 199.

† Trans. 17th N. Amer. Wildlife Conf.: 482.

even though there was no sign of lesions or inflammation. Her hemoglobin value turned out to be very low and she had a white count of over 22,000/cu. mm.

The young fawn, deer No. 61, 6–7 days old, had a very high total white cell count, 26,000/cu. mm., probably as a result of prolonged fright. She had been captured at 11 AM and restrained with her feet tied until she was chloroformed at 8 PM. The blood sample was collected from a jugular vein while she was in the early stages of anaesthesia.

Summary data in Table 2 indicates that the blood picture of the mule deer under the conditions of this investigation is not radically different from that of domesticated livestock.

The results of the *p*H analyses of the stomach and intestine give a more consistent picture than do the blood data. The true stomach is clearly on the acid side (Table 3). Having once passed the pylorus the contents become less acid until at a point twenty to twenty five feet from the stomach they become alkaline and continue so throughout the rest of the tract. The contents of the caecum while still generally alkaline tend to swing toward a neutral *p*H.

The average length of the total gastro-intestinal tract in the female mule deer is about eighty feet. Sisson (THE ANATOMY OF THE DOMESTIC ANIMALS, 1940) reports that the gastro-intestinal tract of the ox is 170 feet; that of the sheep as 95 feet, and the pig as 65 to 80 feet. —LUDVIG G. BROWMAN AND HOWARD S. SEARS, *Department of Zoology, Montana State University, Missoula. Received October 8, 1954.*

REPORT OF DEER ATTACKING COUGAR

The cougar or mountain lion (*Felis concolor*) seems immune to attack by all but the largest predators, such as grizzly bears. As is well known, the principal food of this large cat is deer, and cougars seldom occur where some species of deer is not present. Perhaps it is not surprising that, occasionally, the deer fight back, as one might surmise from the incident reported here. The veracity of this account is open to question, and I have a disinclination to add further to the great mass of myth and legend already associated with the cougar. Still, there are circumstances in this case that suggest its credibility.

On the eastern slopes of Glacier National Park, Glacier County, Montana, the mule deer (*Odocoileus hemionus*) is relatively common. Current estimates place its population at about 800 head. The cougar is present throughout the Park in limited numbers, although it is seldom seen. At the Many Glacier Ranger Station an unidentified camper reported the following episode as occurring on the afternoon of July 1, 1954. The observer was fishing at nearby Redrock Lake when a commotion on the shore attracted his atten.

TABLE 3.—*pH readings of gastro-intestinal tract of female mule deer in Western Montana*

Datum	Deer No.							
	31	32	36	38	53	54	59	Ave.
Date killed	12/12	12/12	12/22	12/22	4/11	4/11	6/11	
Hour killed	9 AM	3 PM	9 AM	1 PM	7 AM	4 PM	11 AM	
Age in years	6½	4½	2½	1½	2½	10 mo.	1	
Gross body wt. in lbs.	117	105	114	102	122	61	72	
C—R length in cms.	130	118	124	126	123	95	99	
Omasum	6.8	6.6	6.2	6.0	5.6	5.9	6.4	6.2
Rumen	6.9	6.6	6.2	5.9	5.8	6.3	6.4	6.3
Abomasum	—	—	3.7	3.6	3.1	3.1	3.4	3.4
Duodenum	4.5	5.6	5.5	5.5	6.0	—	6.5	5.6
First third of small intestine	6.8	—	5.8	6.3	6.4	—	6.6	6.4
Second third, s.i.	—	7.5	8.0	7.0	7.5	—	6.9	7.4
Last third, s.i.	7.3	7.6	7.5	7.8	8.1	—	7.3	7.6
Caecum	7.5	7.2	6.8	6.9	7.0	6.9	7.3	7.1
First half, colon	7.9	6.6	7.1	7.3	7.2	—	7.8	7.3
Last half, colon	8.1	—	7.4	7.5	7.2	7.8	8.0	7.7
Total length, pharynx to anus in feet	—	—	81	86	76	—	72	79

tion. A mule deer doe was launching a vigorous attack on a cougar. Several times she leaped into the air and landed with all four feet on the prostrate cat. At the first opportunity the cat jumped to safety in a tree above, grasping in one leap an overhanging limb seven feet above the ground, as determined by later measurement. No mention was made of the final outcome of the encounter. It was not indicated whether the cougar was an adult or juvenile; nor whether the doe had a fawn nearby, as would seem likely.

The observer had lived in the State of Washington for some fifty years and claimed to be well acquainted with these large, long-tailed cats in the wild. The authenticity of his fragmentary report may well be doubted. However, on July 13 another camper reported seeing what appears to have been a cougar in the same general area, on the south shore of Fishercap Lake, at about 5:00 PM. This man claimed no prior acquaintance with the species, but merely inquired casually if it was common in the area and if it was destructive to other wildlife. His description fitted the big cat perfectly.—RICHARD H. MANVILLE, *Department of Zoology, Michigan State University, East Lansing.* *Received November 1, 1954.*

REVIEWS

Murie, Olaus J. A FIELD GUIDE TO ANIMAL TRACKS. Houghton Mifflin Company, Boston. xxii + 374 pp., 196 figs. + many unnumbered sketches. 1954. Cloth, $3.75.

This is number nine in the well known and widely used Peterson Field Guide Series. Following a brief but informative Editor's Note by Roger T. Peterson, the author presents his acknowledgments. These are followed by the table of contents, a key to tracks and a "life" list of mammals and other animals that are apt to leave sign. The introductory section entitled "What has happened here?" attempts, quite well, to solicit interest in outdoor sleuthing through animal sign. In a humble and matter-of-fact style Murie relates his own field experiences with animals and their spoor. These anecdotes add interest to the subject and command the respect of the reader. The mammals are then covered in phylogenetic order, including some rare, and some domestic species. A brief section is given to birds, amphibians and reptiles, and finally insects and other invertebrates. A selected bibliography of 149 titles is presented. The index of slightly less than six pages covers the scientific and common names of the animals dealt with in the text plus references to gnawing, boring, or clawing of woody plant species, and also a reference to horn and bone chewing. The author has drawn over one thousand black-and-white illustrations to enhance the text. Some of them are cited by bold face numbering in the index which facilitates rapid use of the guide.

The author is a master at making track casts and what he says about preserving tracks will benefit amateur and professional naturalist alike. He states, "I have rarely gone on a field trip in the past twenty-five years without a supply of plaster."

Each animal is sketched in a life pose. Often the anatomical characters that affect the sign are enlarged. Scats of the various higher animals are drawn to a scale. In this respect the author is rivaled only by Seton. Tracks and individual footprints are likewise drawn to scale. Animals within a given group are compared by illustrations of both tracks and scats. This comparative aspect of sign is painstakingly covered so that confusion between tracks of certain animals is reduced to a minimum. To say that this is a book of animal tracks only would be a misleading understatement. One of the book's most outstanding features is the subtle inclusion of pertinent life history and ecology of the animals treated.

This additional information is largely drawn from the extensive field experiences of the author, which adds a flavor of tangibility to the subject that deals largely with where an animal has been. One cannot fail to be impressed with the tremendous amount of original work that has gone into this publication, particularly in light of its high caliber throughout.

The author's art work (pen-and-ink drawings and some scratchboard) can be graded on a normal curve. Some, particularly the arctic hare huddled beside a protecting rock

(p. 234), the domestic cat covering its dung (p. 109), and the foreshortened wolverine in full retreat (p. 68), are exceptionally good. Others such as the burrow mound of the kangaroo rat (p. 170), the white-tailed deer (p. 257), and the birds in general are below par for the author. Texans will be surprised by the passerine appearance of their state bird (p. 326).

There are a few minor faults in even a well-written book such as this one. In point of omission I felt that there should have been a section of general track characters at the beginning of the book. These general principles are scattered throughout the text; for example, that climbing mammals usually have paired front foot tracks when hopping, or that tracks can be identified by an understanding of leg and foot structure. Jaeger in TRACKS AND TRAILCRAFT (Macmillan, 1948) does this very well in acquainting the novice with the animals that walk flat-footed, or on their toes or toe nails.

A number of categorical statements should have been qualified. Murie lists (p. 278) Wisconsin as having moose in its northern counties, when actually there has been only one authenticated moose record in Wisconsin in the last 35 years. Similarly marten are said to occur in the "boreal forests" of the continent. Generally this is true, but specifically Minnesota, Wisconsin, and Michigan, each with some boreal forest areas, do not now include the marten in the current list of resident species. The section on birds, amphibians and reptiles, and insects and other invertebrates is much less inclusive and thorough than the sections on mammals. I hasten to restate that these shortcomings are minor and are diluted in a wealth of excellent and informative field knowledge.

This is the best book on tracks and sign of North American mammals. I recommend it without reservation.—ROBERT A. MCCABE, *Department of Forestry and Wildlife Management, University of Wisconsin, Madison 6.*

RECENT LITERATURE

(Conducted by David H. Johnson, Claude W. Hibbard, Charles P. Lyman, Richard H. Manville, and Henry W. Setzer)

[Reprints of this section may be purchased from the Corresponding Secretary]

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COMMENTS AND NEWS

ZOOLOGICAL NOMENCLATURE: NOTICE OF PROPOSED USE OF THE PLENARY POWERS IN CERTAIN CASES FOR THE AVOIDANCE OF CONFUSION AND THE VALIDATION OF CURRENT NOMENCLATORIAL PRACTICE (A.(n.s.)22)

Notice is hereby given that the possible use by the International Commission on Zoological Nomenclature of its Plenary Powers is involved in applications relating to the under-mentioned names included in Parts 5 and 6 of Volume 11 of the *Bulletin of Zoological Nomenclature*, both of which Parts will be published on 31st May 1955:—

(1) *Application(s) in Part 5 of Volume 11.*

Muntiacus (Class Mammalia), validation of, as from Rafinesque, 1815, with *Cervus muntjak* Zimmermann, 1780, as type species (pp. 167–169) (Z.N.(S.)481)

(2) *Applications in Part 6 of Volume 11.*

gambianus Ogilby, 1835, as published in the combination *Sciurus gambianus* (Class Mammalia), validation of, as the name for the Sun-Squirrel, and designation as the type species of *Heliosciurus* Trouessart, 1880 (pp. 186–188) (Z.N.(S.)909)

silvestris Schreber, [1777], as published in the combination *Felis* (*Catus*) *sylvestris*, validation of, as name for the European Wild Cat. (pp. 189–190) (Z.N.(S.)910)

Phacochoerus Cuvier (F.), 1826 (Class Mammalia), validation of, as generic name for the Wart Hog (pp. 191–195) (Z.N.(S.)756)

Odobenus Brisson, 1760 (Class Mammalia), validation of, as the name for the Walrus (pp. 196–198) (Z.N.(S.)614)

Notice is also given of proposals for the adoption of "Declarations":—

(a) defining the expression "monotypical genus" (pp. 146–152) (Z.N.(S.)904)

(b) defining the combination to be attributed to the specific name for a species described as belonging to one genus but for which at the same time a second nominal genus is established conditionally (pp. 179–180) (Z.N.(S.)894).

Attention is also drawn to the proposed rejection of the generic and specific names given to the so-called "Piltdown Man" as being names given to a fictitious form (pp. 171–172) (Z.N.(S.)883).

Any specialist who may desire to comment on [any of] the foregoing application[s] is invited to do so in writing to the Secretary to the International Commission (Address: 28 Park Village East, Regent's Park, London, N.W.1., England) as soon as possible. Every such comment should be clearly marked with the Commission's File Number as given in the present Notice.

If received in sufficient time before the commencement by the International Commission of voting on the applications in question, comments received in response to the present Notice will be published in the *Bulletin of Zoological Nomenclature*; comments received too late to be so published will be brought to the attention of the International Commission at the time of the commencement of voting on the application in question.

Under the decision by the International Congress of Zoology the period within which comments on the application[s] covered by the present Notice are receivable is a period of six calendar months calculated from the date of publication of the relevant Part of the *Bulletin of Zoological Nomenclature*. The two Parts now in question will be published on 31st of May, 1955. In consequence, any comments on the applications published in these

two Parts should reach the Secretariat of the International Commission at latest by 31st November, 1955.—FRANCIS HEMMING, *Secretary to the International Commission on Zoological Nomenclature.*

DATES OF ISSUE OF PREVIOUS NUMBERS

Correction.—Journal of Mammalogy, Vol. 36, No. 1, was mailed February 25, 1955. Journal of Mammalogy, Vol. 36, No. 2, was mailed May 26, 1955.

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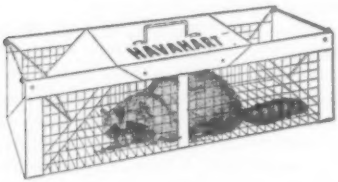

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SUGGESTIONS TO AUTHORS

The *Journal of Mammalogy* publishes original papers with significant new content on any phase of the science of mammalogy. While authors need not necessarily be members of the society, it is suggested that individuals publishing serious papers in this field should consider carefully the desirability of associating themselves with the American Society of Mammalogists.

Papers are generally published in order of receipt with some exceptions at the discretion of the editor. Papers over twenty printed pages in length are rarely published because of costs and limitations of space. When partly subsidized, such papers may occasionally be published at the discretion of the editorial committee.

Photographic illustrations (half-tones) and tabular matter are strictly limited because of high costs of printing. Half-tones for decorative purposes, or interest only, will not be published; they should illustrate some point or fact, best shown in this way, and essential to the exposition of the paper. Tabular matter should contain data not repeated in text.

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